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FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* 74: 627–634.
KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) 2: 309–320.
KOHN, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* 17 (4): 1–51.
THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* 4: 269–270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

(*continued inside back cover*)

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REVISION OF THE LATE VALANGINIAN CEPHALOPODA FROM THE SUNDAYS RIVER FORMATION OF SOUTH AFRICA, WITH SPECIAL REFERENCE TO THE GENUS *OLCOSTEPHANUS*

By

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Cape Town Kaapstad

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By

MICHAEL R. COOPER

*Queen Victoria Museum, Salisbury**

(With 205 figures)

[*MS. accepted 8 August 1980*]

ABSTRACT

The cephalopod fauna from the Sundays River Formation is revised and shown to comprise 14 species and varieties of *Olcostephanus*, 2 species each of *Distoloceras*, *Bochianites* and *Belemnopsis*, and 1 species each of *Neohoploceras*, *Eodesmoceras*, *Partschiceras*, and *Eutrephoceras*. Sexual dimorphism is recognized within *Olcostephanus* and the implications and importance of this phenomenon are discussed at length. The fauna is considered of latest Valanginian (*O. baini* Zone) age. The new genus *Jeanthieuloyites* is proposed for *Rogersites quinquestriatus* Besairie, and one new species of *Olcostephanus*, *O. riccardii* sp. nov., is described.

CONTENTS

INTRODUCTION

In the southern and south-eastern Cape, late Mesozoic sediments occur as a widely scattered series of basins, representing basin infills in uneven terrain. The bulk of these deposits are of non-marine origin, and it is only in the Uitenhage basin (Fig. 1), where these sediments attain their fullest development,

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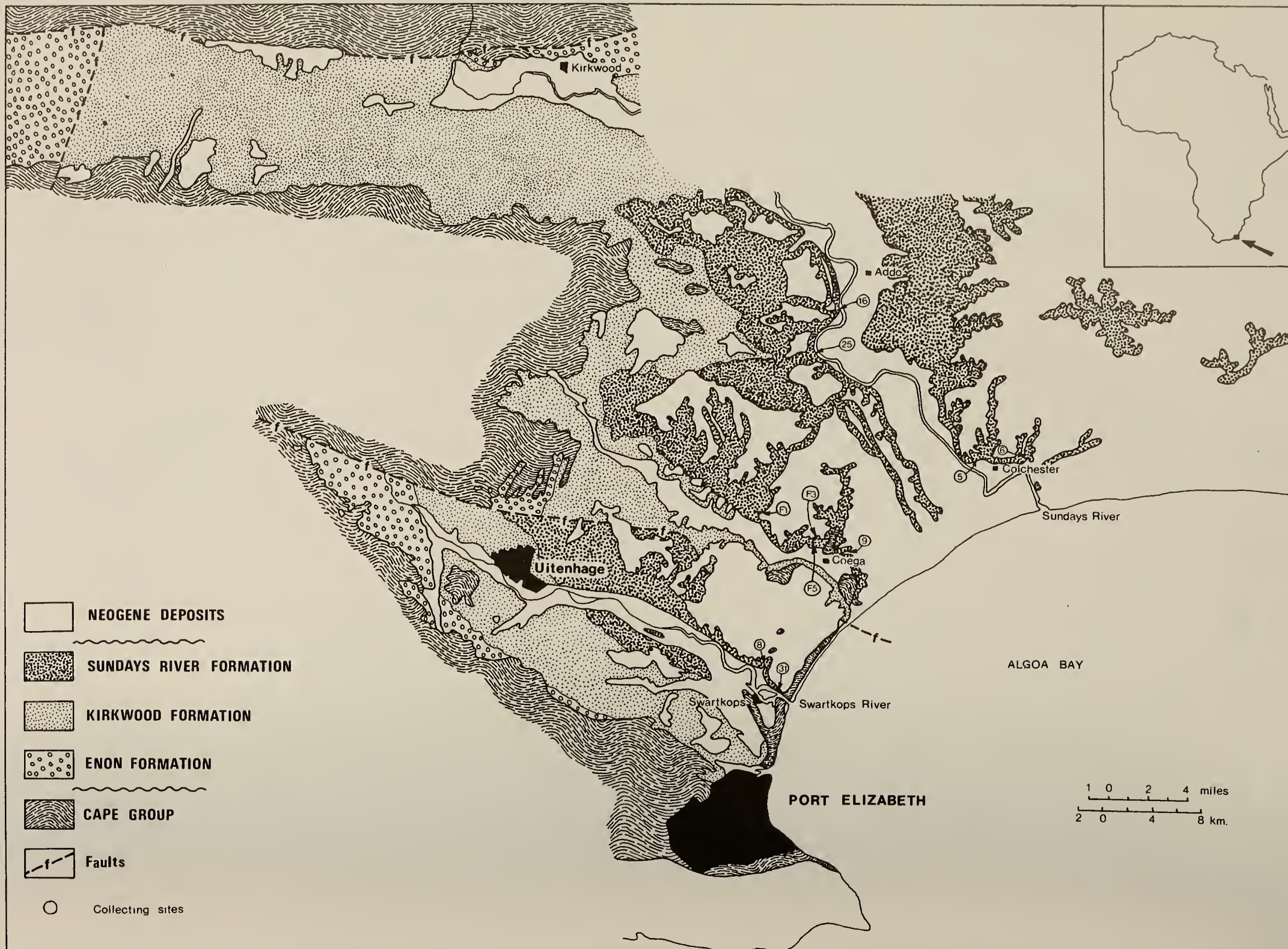

Fig. 1. The geology of the Uitenhage Basin (after Geological Survey Map of 1962).

that the succession is complete. It was to the sediments of this area that Tate (1867) first applied the name 'Uitenhage Beds'.

Within the sediments of the Uitenhage Group (Winter 1973), a tripartite subdivision has long been recognized which, using current lithostratigraphic nomenclature, is:

3. Sundays River Formation
2. Kirkwood Formation
1. Enon Formation

With the break-up Gondwanaland, the depositional history of the area was initially one of rapid deposition of fluviatile sandstones and torrential conglomerates of the Enon Formation, followed by the more quiescent, lagoonal to marginally marine environments of the Kirkwood Formation, finally terminating in the transgressive marine deposits of the Sundays River Formation. It is the rich invertebrate faunas of the latter unit that have provided the main basis for the dating of the Uitenhage Group.

Fossils were first recorded from the Uitenhage Group by Hausmann (1837) who described some molluscs from the Sundays River valley, including the ammonites *Ammonites spinosissimum* and a '*Hamites*' sp., the latter being erroneously compared with the late Albian species *H. intermedius* J. Sowerby and *H. funatus* Brongniart. He considered the fauna to be of Lower Cretaceous age, a determination supported by Goldfuss (1837, 1840) who figured two of Hausmann's shells, whilst Krauss (1843, 1850) assigned a Neocomian age to a small collection of bivalves from the Swartkops River.

In 1851 Portlock (1852) exhibited a collection of fossil plants and molluscs, collected by Rubidge from the Sundays River valley, to which he assigned a probable Jurassic age.

Bain (1856) doubtfully referred the Uitenhage fossils to the Lias, based on the abundance of the supposedly Liassic form, '*Gryphaea incurva*', actually a misidentification of *Aetostreon imbricatum* (Krauss). In an appendix to Bain's paper, Sharpe described a new collection of fossils from the Sundays and Swartkops Rivers, including the ammonites *Ammonites atherstoni* and *A. baini*. An erroneous comparison of these two species with 'Lower Oolite' (Bajocian) forms led Sharpe to conclude that the fauna was most closely related to those from the 'Lower and Middle Oolite' (Bajocian–Bathonian) of Europe.

In 1857 Atherstone suggested a partly Jurassic and partly Cretaceous age for the Uitenhage Group, although Wyley (1859) placed the Enon Formation as low as the New Red Sandstone (Triassic) and correlated the Sundays River Formation with the 'Oolites' (Middle Jurassic).

In his description of several new molluscs from the Uitenhage Group, Tate (1867) considered the deposit to represent a condensed sequence spanning the entire Jurassic period, with the possible exception of the 'Upper Oolite'. Amongst the new forms described were *Ammonites subanceps*, compared with *A. anceps* Reinecke from the 'Middle Oolite' (a Callovian *Reineckia*), *Hamites*

africanus, and the belemnite *Belemnites africanus* which was compared with the Jurassic *B. aucklandicus.*

Stoliczka (1871), in his monograph of the Cretaceous Bivalvia of southern India, suggested that some of the Uitenhage forms showed Cretaceous rather than Jurassic affinities.

The bivalve *Crassatella complicata* Tate was assigned by Dames (1873) to the genus *Ptychomya* and considered to indicate a Neocomian age, a suggestion supported by a fragment of ammonite which Dames believed to be identical with *Ammonites astieri* d'Orbigny.

Lycett (1879), in the concluding chapter of his monograph of the British fossil trigoniids, expressed the opinion that some of the more characteristic of the Uitenhage forms pointed decisively to a Cretaceous age.

In a critical review of Tate's work, Neumayr (*in* Holub & Neumayr, 1882), besides describing several new bivalves and figuring the holotype of *Crioceras spinosissimum* (Hausmann) for the first time, dealt with the age of the Sundays River faunas at some length. He considered *Olcostephanus atherstoni* (Sharpe), *O. baini* (Sharpe), '*Crioceras*' *spinosissimum* (Hausmann), '*Trigonia*' *ventricosa* Krauss, '*T*'. *conocardiiformis* Krauss, *Crassatella complicata* Tate, and '*Exogyra*' *imbricata* Krauss to be essentially Cretaceous in character. He also considered Tate's *Ammonites subanceps* to possibly represent merely the juvenile whorls of *Crioceras spinosissimum.*

Griesbach (1880), Jones (1884), Moulle (1885), Futterer (1897), and Molengraaf (1900) all assigned a Jurassic age to the Uitenhage Group, while Gürich (1887), Schenk (1888), Molengraaf (1890), and Lemoine (1906), on the other hand, suggested a Lower Cretaceous age.

Pavlow (*in* Pavlow & Lamplugh 1892) assigned both *Ammonites atherstoni* and *A. baini* to the Neocomian subgenus *Holcostephanus* (*Astieria*), thereby suggesting a Lower Cretaceous age for the Sundays River Formation. Moreover, he considered *H. atherstoni* (Sharpe) to be identical to *H. psilostomus* (Neumayr & Uhlig) from northern Germany.

Newton (1896) published a complete list of the known Mollusca from the Uitenhage Group and assigned them a Neocomian age, while Passarge (1904) suggested an Upper Jurassic–Lower Cretaceous age.

Kitchin (1908), in his exhaustive study, gave a concise treatment of the earlier literature and dealt with the age of the fauna at great length. He considered the Cephalopoda to carry the greatest weight in the assignment of an age to the deposit, noting that '. . . the known species of *Holcostephanus* (*sensu stricto*) are almost wholly, if not entirely, confined to strata of Upper Valanginian and Lower Hauterivian age' (p. 30). Having shown that Tate's comparison of many of the Bivalvia with Jurassic forms was erroneous, Kitchin (1908: 39) was led to conclude '. . . that no portion of the Uitenhage Series represents a period of time earlier or later than the Neocomian. It must be said, indeed, that the almost entire restriction of *Holcostephanus sensu stricto* (= *Astieria* Auctorum), to the upper part of the Valanginian and the lower

beds of the Hauterivian in Europe suggests much narrower limits, when we consider how important a place is taken by members of this genus in characterizing the cephalopod-fauna of the Uitenhage beds.' Amongst the ammonites, Kitchin (1908) described six new species—*Bochianites glaber*, *Phylloceras rogersi*, *Holcostephanus wilmanae*, *H. modderensis*, *H. rogersi*, and *H. uitenhagensis*, as well as referring to a *Belemnites* sp. from Coega.

Wegner (1909), in a review of the subgenus *Holcostephanus* (*Astieria*) into which he included all the Uitenhage forms, accepted the majority of these as valid, with the exception of *H. wilmanae* which he considered to represent a variety of *H.* (*Astieria*) *psilostomus* Neumayr & Uhlig.

In 1924 Spath erected the new genus *Rogersites*, type species *R. modderensis* (Kitchin), to include all the Olcostephaninae from the Uitenhage Group without, however, providing a formal diagnosis.

In a revision of the Uitenhage Cephalopoda in 1930, Spath had still not formulated a generic diagnosis for *Rogersites*, but included into it all previously described olcostephanids from the Uitenhage Group, as well as describing the new species *Rogersites kitchini*, *R. crassicostatus*, *R. sphaeroidalis*, *R. otoitoides*, *Eodesmoceras haughtoni* and the nautiloid *Eutrephoceras uitenhagense*.

AGE OF THE SUNDAYS RIVER FORMATION

Kitchin's (1908) detailed study of the faunas from the Sundays River Formation dispelled any doubt as to the presence of Jurassic forms, while concluding that '. . . the Marine Beds represent not more than the strata at the top of the Valanginian and the base of the Hauterivian'.

Besairie (1936) and Collignon (1962) have recorded rich olcostephanid faunas from Madagascar which include *Olcostephanus atherstoni* (Sharpe), *O. baini* (Sharpe), *O. uhligi* (Collignon) (= *O. fascigerus* Spath), and *Distoloceras spinosissimum* (Hausmann) from the Valanginian of that island. *Partschiceras rogersi* (Kitchin), the type of which was collected midway up the cliffs behind Colchester, and thus high in the marine succession, is reported by Collignon (1962) only from the Lower Valanginian, although Haughton (1963) mentions its occurrence in strata of early Hauterivian age from the same island. Like most phylloceratids, therefore, it is presumably a long-ranging species of little use for detailed biostratigraphic correlation.

Böse (1923) and Imlay (1937, 1938, 1940, 1960) have recorded rich olcostephanid faunas from the Upper Valanginian and Lower Hauterivian of Mexico. Imlay (1937, 1938) considered the upper part of the Taraises Formation to be of early Hauterivian age. His faunal list from these beds included *Olcostephanus*, *Maderia*, *Mexicanoceras*, *Acanthodiscus*, *Leopoldia*, *Neocomites*, *Distoloceras*, *Valanginites*, *Thurmannites* (= *Thurmanniceras*), *Bochianites*, *Kilianella*, and *Dichotomites*. The pyritic olcostephanid nuclei *Maderia* and *Mexicanoceras* are endemic and of no value in biostratigraphic correlation. According to Wright (*in* Arkell *et al.* 1957), *Neocomites*, *Thurmanniceras*,

Valanginites, and possibly *Kilianella* are all restricted to Valanginian and older strata. A somewhat older age is also suggested for the lower portion of the Upper Member of the Taraises Formation by the faunal association *Olcostephanus–Bochianites–Distoloceras*, which characterizes the Upper Valanginian of Speeton (England), Verdon (France) and Madagascar, as well as being typical of the Uitenhage Formation. This is supported by the presence of *Kilianella mayranensis* Imlay which closely resembles *K. roubaudiana* (d'Orbigny), the differences hardly warranting specific separation. It seems likely, therefore, that Imlay's fauna should be considered as having come from more than one palaeontological zone, including Upper Valanginian strata.

A re-examination of the Valanginian stratotype led Barbier & Thieuloy (1963) to subdivide the Valanginian into a lower *Kilianella roubaudiana* Zone and an upper *Saynoceras verrucosum* Zone. The so-called 'Astieriaschicht', rich in *Olcostephanus atherstoni* (Sharpe) (Barbier & Thieuloy 1963: 82), is placed at the top of the Valanginian, pending detailed reinvestigation. In 1967, however, Moullade & Thieuloy wrote '. . . il subsiste cependant toujours un large hiatus non caractérisé par les Ammonites entre le Valanginien 'moyen' à *Saynoceras verrucosum* et les termes ultimes du Valanginien supérieur'. The terminal Valanginian was subdivided into a lower zone of *Himantoceras trinodosum* (Thieuloy) and an upper zone of *Sarasinella ambigua* (Uhlig), while the base of the Hauterivian was marked by the appearance of *Acanthodiscus radiatus* (Brugière).

Busnardo & Cotillon (1964) recorded a rich olcostephanid fauna from Bas–Verdon in France, from calcareous marls at the very top of the Valanginian, overlain by so-called Valanginian–Hauterivian passage beds, in turn succeeded by Lower Hauterivian beds with *Acanthodiscus radiatus*, *Olcostephanus filosus* (Baumberger) and *O.* aff. *psilostomus* (Neumayr & Uhlig). The Upper Valanginian fauna included *O. atherstoni* (Sharpe).

In Argentina, strata with *O. atherstoni* (Sharpe) are apparently overlain (Riccardi *et al.* 1971) by a Lower Hauterivian faunal assemblage with *Acanthodiscus* cf. *radiatus* (Brugière). Riccardi *et al.* (1971) believed their fauna to show close agreement with the 'Astieriaschicht' of the Swiss Jura, but preferred tentatively to date the Argentinian *Olcostephanus atherstoni* assemblage at '. . . late Valanginian to earliest Hauterivian, pending detailed biostratigraphic revision on a world-wide scale'.

At Speeton (Spath 1924) there is an apparent hiatus, possibly only local, during the Upper Valanginian–basal Hauterivian, and derived fossils of this age occur in the black nodules of Division D_2. Spath (1924: 86) considered '. . . the main development of *Olcostephanus*, of which *A. astieri* is the genotype, is at the base of the Hauterivian and uppermost Valanginian'.

The top bed of the Middle Member of the Chichali Formation in the Trans Indus Range of northern Pakistan has yielded a rich *Olcostephanus* fauna (Spath 1939; Fatmi 1977) which leaves little doubt as to its contemporaneity with the Sundays River faunas. Species in common include *O. fascigerus*

Spath, *O. baini baini* (Tate), *O. baini* var. *sphaeroidalis* (Spath), *O. rogersi* (Spath), and perhaps *O. densicostatus* (Wegner) and *O. perinflatus* (Matheron).

Imlay & Jones (1970) recorded *Olcostephanus* cf. *O. atherstoni* Baumberger (*non* Sharpe) (=? *O. baini* (Sharpe)) from the zone of *Buchia keyserlingi* (Lahusen) in Oregon, considered to be of Middle to Upper Valanginian age, and associated with the genera *Bochianites*, *Neocomites*, *Thurmanniceras*, *Neocraspedites*, and *Polyptychites*.

From Fernão Velosa, in northern Mozambique, Spath (1930) has recorded *Olcostephanus schenki* (Oppel) (= *O. baini* (Sharpe)), and *Haploceras* (*Neolissoceras*) cf. *grasianum* (d'Orbigny). Strata of a similar age also crops out at Mahiba Hill, to the west of Port Amelia, where Newton (1924) recorded fragments of *Lytoceras* together with the belemnite *Duvalia*. From this same locality Spath (1930: 134) also records a '. . . portion of the periphery of a Neocomitid (*Lyticoceras* of the type of *L. regalis* (Bean) or *Neocomites neocomiensis* (d'Orbigny) as figured by Sayn), and the impression of a fragment of the Uitenhage *Bochianites africanus* are decisive and unmistakable'.

The coarse ribbing of the olcostephanids from the Uitenhage Group has long been a distinctive feature. It is of interest to note, therefore, that where the basal Hauterivian is best known (Debelmas & Thieuloy 1963), the associated species of *Olcostephanus* are frequently finely and densely ribbed, with such taxa as *O. filosus* (Baumberger) and *O. sayni* (Kilian) common. *Olcostephanus atherstoni* (Sharpe) also occurs but, as will be shown, represents a stock-name for a number of homoeomorphic macroconchs. The absence of such finely ribbed forms, together with *Acanthodiscus*, from the Sundays River Formation supports the suggestion that this unit should be considered of latest Valanginian age only.

In order to help resolve the Valanginian–Hauterivian boundary problem, it seems necessary to introduce a zone of *Olcostephanus baini* at the top of the Valanginian (Collignon 1962). The following Valanginian–Lower Hauterivian zonal scheme would appear to be of global significance:

Lower Hauterivian	*Crioceratites duvali* *Acanthodiscus radiatus*
Valanginian	*Olcostephanus baini* *Saynoceras verrucosum* *Kilianella roubaudiana* *Thurmanniceras thurmanni*

The Uitenhage fauna may be assigned, therefore, to the assemblage zone of *O. baini*. Besides the Uitenhage species described herein, other important elements of the zone include *Neocomites* spp, *Himantoceras* spp, *Neohoploceras* spp, *Distoloceras* spp, *Sarasinella* spp, *Leopoldia* spp, *Bochianites* spp, *Olcostephanus* spp, together with the less diagnostic *Hemilytoceras liebigi* (Oppel), *Haploceras* (*Neolissoceras*) *grasianum* (d'Orbigny), *Phylloceras thetys* (d'Orbigny), *P. serum* (Oppel) and so on.

SYSTEMATICS

A revision of the Uitenhage ammonite fauna, characterized by the abundance of forms assigned to the genus *Olcostephanus*, some of which have attained unusually large size, has long been overdue, especially in view of the recognition of sexual dimorphism within many groups of the Perisphinctaceae, and more recently in the genus *Olcostephanus* itself (Riccardi *et al.* 1971). Moreover, the erection of numerous species (and genera) within the Olcostephaninae, based upon subtle and generally insignificant differences with no regard for intraspecific variation, has led not only to taxonomic chaos but also to difficulties in interregional correlation.

The following abbreviations are used to indicate the source of the material:

AM	Albany Museum, Grahamstown
BM	British Museum (Natural History), London
LJE, AAS	Geological Survey, Pretoria
MNHP	Natural History Museum, Paris
OUM	Oxford University Museum, Oxford
PEM	Port Elizabeth Museum, Port Elizabeth

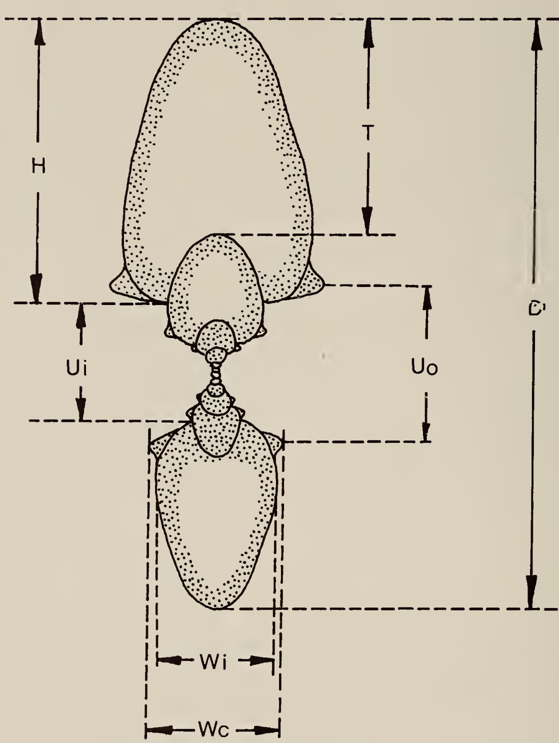

Fig. 2. Schematic diagram showing the measurements discussed in the text.

The abbreviations for measurements given in the text are explained in Figure 2 where D = diameter, H = height, Uo = outer umbilical diameter (between umbilical bullae), Ui = inner umbilical diameter (between umbilical seams), Wi = intercostal width. All measurements are given in millimetres, and dimensions, as a percentage of the diameter, are included in parentheses.

Class CEPHALOPODA Cuvier, 1797

Subclass AMMONOIDEA Zittel, 1884

Order PHYLLOCERATIDA Arkell, 1950

Superfamily PHYLLOCERATACEAE Zittel, 1884

Family **Phylloceratidae** Zittel, 1884

Subfamily Phylloceratinae Zittel, 1884

Genus *Partschiceras* Fucini, 1920

Type species *Ammonites partschi* Stur, 1851 (*non* Klipstein 1843);
by original designation of Fucini, 1920

Discussion

This is a long-ranging genus, having been recorded from Lower Jurassic (Sinemurian) to Upper Cretaceous (Maastrichtian). It differs from *Phylloceras* in being more inflated with maximum width at mid-flank, and in commonly developing ribs as well as lirae in maturity. Moreover, *Phylloceras* has triphyllic saddles not diphyllic as in *Partschiceras*. Wiedmann (1962 has recently included *Phyllopachyceras* Spath as a junior synonym in this genus.

Partschiceras rogersi (Kitchin, 1908)

Fig. 3

Phylloceras rogersi Kitchin, 1908: 179, pl. 8 (fig. 19, 19a–c). Spath, 1930: 140. Du Toit, 1954: 384. Haughton, 1963: 274.

Non Phylloceras rogersi Kitchin var. nov., Krenkel, 1910: 223, pl. 22 (fig. 9) (= *P. krenkeli* Zwierzycki).

Phyllopachyceras rogersi (Kitchin) Collignon, 1962: 20, pl. 181 (figs 815–816).

Material

The holotype is the only example so far collected from the Sundays River Formation and its present whereabouts is unknown.

Fig. 3. *Partschiceras rogersi* (Kitchin). The holotype, by monotypy, with part of the suture (after Kitchin 1908). × 1.

Holotype

By monotypy, the original of the specimen figured by Kitchin (1908: 179, pl. 8 (fig. 19, 19a–c)), from the Sundays River Formation, mid-way up the cliffs behind Colchester.

Diagnosis

An immature *Partschiceras* of late Valanginian age characterized by extremely fine, dense lirae, with no sign of ribbing.

Description

A rather inflated, very involute form, with slightly convex flanks and maximum width at mid-flank. Ornament comprises fine, prorsiradiate, flexuous ribs. At a whorl height of 9 mm there are 12 ribs within a 2 mm distance along the venter.

Discussion

Kitchin's holotype, the whereabouts of which is not known, still remains the only record of this species (and genus) from the Sundays River Formation. Since this specimen appears to be immature and the coarse ribbing of this genus appears typically in maturity, the validity of this species is in doubt.

Partschiceras infundibulum (d'Orbigny) appears to be more compressed, whilst also possessing the coarse ribbing not seen in the Uitenhage example.

Phylloceras krenkeli Zwierzycki was established for the specimen figured by Krenkel (1910: 223, pl. 22 (fig. 9)) as *P. rogersi* var. nov., and said to differ from the Uitenhage species in being more compressed, with the greatest width at the umbilical margin and not at mid-flank, having a different suture, and in being more coarsely ribbed, with only eight ribs within a 2 mm distance.

Occurrence

The holotype was collected from mid-way up the cliffs behind Colchester, and thus near the top of the marine succession.

Collignon (1962) has recorded this species from the Lower Valanginian of Madagascar, while Haughton (1963) mentions its occurrence in beds of Lower Hauterivian age from the same island. It would seem, therefore, that *P. rogersi*, like many phylloceratids, is a relatively long-ranging species.

Suborder Ancyloceratina Wiedmann, 1966
Superfamily ancyloceratACEAE Meek, 1876
Family **Bochianitidae** Spath, 1922
Subfamily Bochianitinae Spath, 1922
Genus *Bochianites* Lory, 1898

Type species *Baculites neocomiensis* d'Orbigny, 1842;
by original designation of Lory, 1898.

Discussion

This is a relatively long-ranging genus, having been recorded from Tithonian to Hauterivian strata. *Janenschites* was said to have a more denticulate suture

than *Bochianites* with long elements, but similar ornament. It has, however, recently (Wiedmann 1962) been included in the synonymy of *Bochianites*.

Bochianites glaber Kitchin, 1908

Fig. 4

Bochianites glaber Kitchin, 1908: 181, pl. 8 (figs 20–21). Hatch & Corstorphine, 1909: 303 fig. 75f. Spath, 1930: 155. Du Toit, 1954: 384. Klinger & Kennedy 1979: 17.

Material

The lectotype, SAM–4695, with some fragments crowded together in the same block of matrix (SAM–12736) from *c.* 2 km upstream from the Swartkops bridge.

Holotype

By lectotype designation herein, the original of *Bochianites glaber* figured by Kitchin (1908: 181, pl. 8 (fig. 20)) from the road below the railway cutting, *c.* 2 km from Rawson bridge on the main line in the Swartkops River Valley.

Fig. 4. *Bochianites glaber* Kitchin. A. Ventral view of the lectotype, SAM–4695, × 4. B–C. Ventral and lateral views of the lectotype, × 3.

Diagnosis

A small, very finely ribbed, juvenile *Bochianites*, with an elliptical whorl section at the largest known growth stages.

Description

A small, slowly expanding *Bochianites*, with an initially circular whorl section, becoming elliptical with age. Ornament comprises fine, prorsiradiate lirae, arching across the siphonal line and straight or slightly convex adapically across the dorsum.

Discussion

A number of fragmentary straight shafts within a single block of matrix would seem to belong to this species, the fine ribbing only becoming visible under a hand-lens. No constrictions were observed.

Baculites maldonadi Karsten (1856: 105, pl. 2 (fig. 2)) (Fig. 5) approaches

Fig. 5. *Baculites maldonadi* Karsten (after Karsten 1856). × 1.

the present species but as they represent different growth stages comparison is difficult. The adapical portion of Karsten's species shows the same thread-like ribbing as *B. glaber*, but adorally it coarsens considerably to resemble *B. africanus*.

Whilst there are a number of other *Bochianites* species with which *B. glaber* might be compared, the immature nature and poor preservation of the South African material make such comparisons unwarranted. Indeed, *B. glaber* might even represent the earliest growth stages of *Umgazaniceras thieuloyi* Klinger & Kennedy (1979: 12, figs 1–2, 3A–D, 4–5). As such it is perhaps best regarded as a *nomen dubium*.

Occurrence

At present *B. glaber* is known only from the Sundays River Formation and is thus of latest Valanginian age.

Bochianites africanus (Tate, 1867)

Figs 6–7

Hamites africanus Tate, 1867: 150, pl. 7 (fig. 5). Holub & Neumayr, 1882: 271.

Bochianites africanus (Tate) Kitchin, 1908: 225. Spath, 1930: 153, pl. 14 (figs 2–3), pl. 15 (fig. 3). Du Toit, 1954: 384. Klinger & Kennedy, 1979: 17, fig. 3F–H.

Material

Numerous specimens, including BM–C25227–9, AM–844, 846, SAM–PCU1586–88, 5706, and 12784–88.

Holotype

By the lectotype designation of Spath (1930), the original of Tate's (1867) plate 7, figure 5a, BM–C25228, from Prince Alfred's Rest at the Sundays River mouth.

Diagnosis

A coarsely ribbed species of *Bochianites* with 4–7 prorsiradiate ribs in a distance equal to twice the whorl width and an elliptical to subtrigonal whorl section.

Fig. 6. *Bochianites africanus* (Tate) The syntypes, of which the top right-hand specimen was selected as lectotype (after Tate 1867; composite suture after Spath 1930). × 1.

Description

A slowly expanding, coarsely ribbed *Bochianites* with an elliptical whorl section in immaturity, becoming subtrigonal at large sizes when the maximum width is near the dorsal shoulders. The dorsum is flattened in all but the youngest individuals. Ornament comprises coarse annular ribs, strongly projected on the flanks and sharply arched across the venter. Because of the oblique angle at which the ribbing crosses the distinctly tabulate venter of mature individuals, the ribs are broadest across the venter as well as being asymmetrical with a gentle adapical slope and a steep adoral slope. Rib density varies between 4 and 7 in a distance equal to twice the costal whorl width.

Discussion

Bochianites africanus (Tate) is closest to *B. neocomiensis* (d'Orbigny) (1842*a*, pl. 138 (figs 1–5)) which has, however, an almost perfectly circular whorl section. Spath (1930: 154) considered the present species to be very close to *Baculites granatensis* Karsten (1856: 105, pl. 2 (fig. 1)), to which illustration it certainly bears a considerable resemblance but, according to J.-P. Thieuloy (*in litt.* 1980), the Columbian species (Fig. 8) is a late Cretaceous *Baculites*.

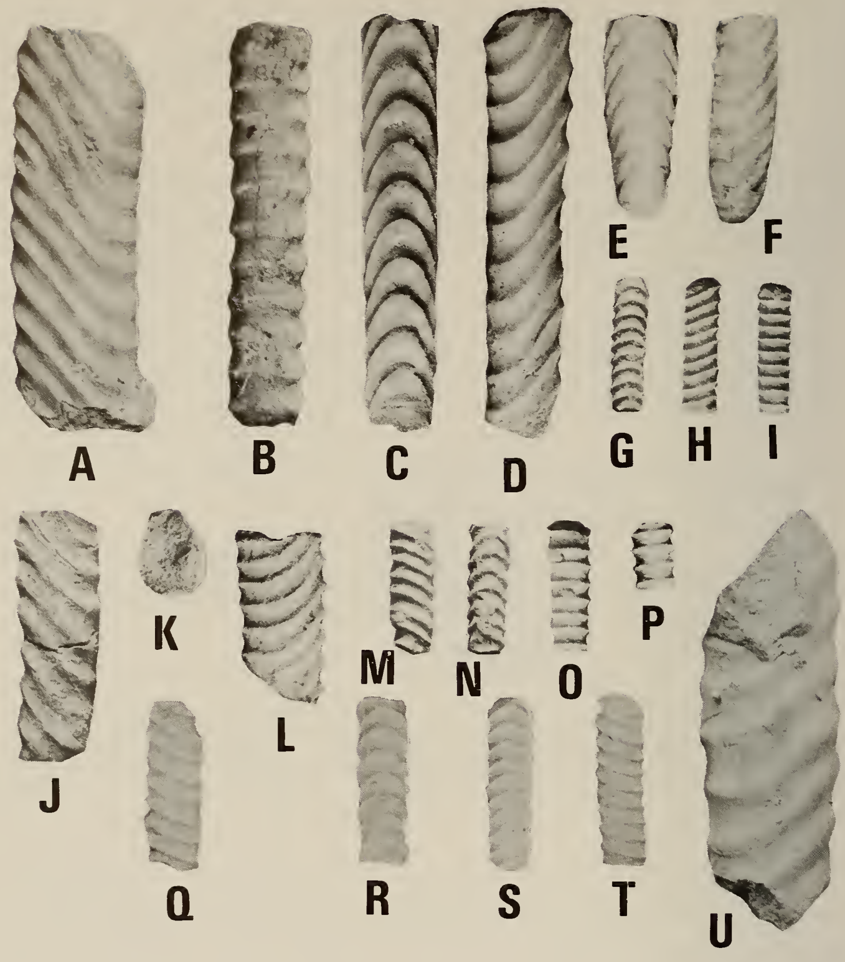

Fig. 7. *Bochianites africanus* (Tate). A. Lateral view of AM–844, × 0,75. B–D. Dorsal, ventral and lateral views of AM–846, × 0,75. E–F. Lateral and ventral views of AM–868, × 0,75. G–I. Ventral, lateral and dorsal views of a specimen in the South African Museum, × 1. J–K. Lateral and cross-sectional views of an unnumbered specimen in the South African Museum, × 0,75. L. Lateral view of SAM–PCU1586, × 1. M–O. Lateral, ventral and dorsal views of a specimen in the South African Museum, × 1. P. Dorsal view of SAM–PCU1587, × 1. Q–R. Lateral and ventral views of a specimen in the South African Museum, × 1. S–T. Ventral and lateral views of a specimen in the South African Museum, × 1. U. Lateral view of an unnumbered specimen in the South African Museum, × 1.

Fig. 8. *Baculites granatensis* Karsten (after Karsten 1856). × 1.

Imlay (1938: 585, pl. 6 (figs 1,11–13)) figured specimens of a *Bochianites* sp. from the Upper Member of the Taraises Formation which he compared with *B. neocomiensis* (d'Orbigny). The ornament is closely comparable with that of *B. africanus*, but since the whorl section was not figured or mentioned its specific assignment is unknown.

Occurrence

Bochianites africanus (Tate) is as yet known only from northern Mozambique and South Africa. It seems surprising that it has not yet been recorded from Madagascar in view of the relative abundance of this species in the Sundays River Formation.

Superfamily PERISPHINCTACEAE Steinmann, 1890

Family **Olcostephanidae** Haug, 1910

Subfamily Olcostephaninae Haug, 1910

Genus *Olcostephanus* Neumayr, 1875

Type species *Ammonites astieri* d'Orbigny, 1840;
by original designation of Neumayr, 1875.

1875 *Olcostephanus* Neumayr
1889 *Holcostephanus* Sayn
1892 *Astieria* Pavlow
1923*a* *Subastieria* Spath
1923*b* *Parastieria* Spath
1924 *Rogersites* Spath
1938 *Mexicanoceras* Imlay
1938 *Maderia* Imlay
1964 *Jeannoticeras* Thieuloy
1966 *Taraisites* Cantu Chapa
1966 *Satoites* Cantu Chapa
1977*a* *Lemurostephanus* Thieuloy

Emended diagnosis

Compressed to strongly inflated cadicones, with strongly arched to well-rounded venters. Primary ribs are usually present on the umbilical wall, commonly terminating in tubercles at the umbilical shoulder (except on the outer whorls of *Parastieria* and *Jeannoticeras*), from which arise straight or slightly curved secondary ribs, usually in fasciculate bundles (in pairs in *Jeannoticeras*). There are commonly 3–4 secondaries per bundle, although there may be as many as 6–9 or as few as 1–2. Secondary ribs may bifurcate on the flanks, while intercalated ribs between bundles are the rule. Ribbing generally passes uninterrupted across the venter, although it may weaken considerably where a ventral furrow is present (i.e. *Mexicanoceras*). Parabolae may or may not be present, but never on the outer whorls of females. This genus is dimorphic; males small and with lappets, females larger and with simple peristomes. Age: Upper Valanginian–Middle Hauterivian.

Discussion

In addition to the objective synonyms *Holcostephanus* and *Astieria*, Wiedmann & Dieni (1968) also placed *Rogersites* within *Olcostephanus* s.s., as well as including *Parastieria* and *Subastieria* within the genus as subgenera. *Capeloites* was considered by these authors to be of dubious status, but, as since shown by Thieuloy (1969), is distinct.

In 1924 Spath erected the new genus *Rogersites*, types species *R. modderensis* (Kitchin), without giving a formal diagnosis. In his revision of the Uitenhage Cephalopoda in 1930, Spath had still not formulated a generic diagnosis for *Rogersites*, but included into it all previously described olcostephanids from the Uitenhage Group. In his monograph of the Cephalopoda of the Neocomian Belemnite Beds of the Salt Range, he (Spath 1939: 11) diagnosed *Rogersites*, stating that '. . . although there are no typical *Rogersites* (e.g. *R. modderensis* Kitchin sp., *R. baini* Sharpe sp. and *R. kitchini* Spath), with few and very coarse primary and secondary ribs and prominent umbilical edge', while further on (p. 31) he refers to '. . . the typical *Rogersites* characters, namely a coronate cadicone and vertical umbilical wall, at large diameters, while retaining coarse ribbing'. At this time Spath was using *Rogersites* both as a genus and a subgenus. Thus (Spath 1939: 11), '. . . there is one common and widely quoted transitional species between *Rogersites* and *Olcostephanus*. This is *O.* (*Rogersites*) *schenki* (Oppel)'. On page 16 he refers to *Rogersites sphaeroidalis* and *R. atherstoni*, but on page 19 states '. . . I previously referred *O. uitenhagensis* to *Rogersites*, but like *R. atherstoni*, *R. sphaeroidalis* and the many passage forms between these species, *O. uitenhagensis* is one of the transitions from *Rogersites* to *Olcostephanus*'. On page 31 Spath states '. . . *O.* (*R.*) *schenki* is the most strongly and distantly ribbed form of *Olcostephanus* from the Salt Range and the only species that may be compared with such typical *Rogersites* as *R. modderensis* (Kitchin). . . . Since however, no large examples of *O. schenki* have yet been found or recognized, it is uncertain whether it develops the typical *Rogersites* characters.'

Imlay (1938) erected three new genera, all comprising entirely septate pyritic nuclei, within the Olcostephanidae, viz. *Maderia*, *Mexicanoceras*, and *Ceratotuberculus*. *Mexicanoceras* was considered '. . . similar in form, sculpture and suture-line to *Olcostephanus*. It differs from *Olcostephanus* in having a ventral furrow on the outer whorls, a more inflated form, broader whorl section, and its much smaller size.' These features are herein considered of only subgeneric value and *Mexicanoceras* is accordingly placed within *Olcostephanus* s. l. *Maderia* was defined by Imlay (1938) as '. . . similar to *Subastieria* (defined by Spath, 1923, p. 32) but exhibits a slight thinning of the ribs along the midventral line of the outer whorls. Compared with *Mexicanoceras* its whorl section is more depressed, its umbilicus wider, and the ventral thinning of the ribs less pronounced.' The importance attached to the very slight weakening of the ribs across the siphonal line in *Maderia* by Imlay (1938) appears unjustified and, in the author's opinion, *Maderia* comprises an heterogeneous assemblage

of *Olcostephanus* s.s. and possibly *O.* (*Subastieria*), and is, therefore, superfluous. The genus *Ceratotuberculus* is characterized by the appearance, after the third whorl, of high, thick, ventrolateral bullae, as well as by possessing a ventral furrow, whilst retaining the other olcostephanid characters. If, as suggested by Imlay (1938), this genus is of early Hauterivian age, then it is probably descended from *Saynoceras.* If, however, it is of late Valanginian age, then the differences probably warrant at most subgeneric separation from *Saynoceras.*

Spath (1924) erected the genus *Subastieria* for *Olcostephanus sulcosus* Pavlow, differentiated from *Olcostephanus* by its younger age and highly coronate whorl section. According to Wright (*in* Arkell *et al.* 1957), *Subastieria* closely resembles the inner whorls of some *Rogersites* which, as just shown, is a synonym of *Olcostephanus* s.s. Moreover, Wiedmann & Dieni (1968) have recently shown *Subastieria* to range into the Upper Valanginian, whilst *Olcostephanus* is common in the Lower Hauterivian of the Swiss Jura (Debelmas & Thieuloy 1963). Consequently, not only do *Subastieria* and *Olcostephanus* have the same stratigraphic range, but they are also morphologically very similar. However, in *Subastieria* the whorl section is coronate at all growth stages, whereas microconch forms of *Olcostephanus* become coronate only with the egression of the umbilical seam on the body chamber. This appears to be a subtle but distinct difference, and consequently Wiedmann & Dieni (1968) are provisionally followed in treating it as a valid subgenus.

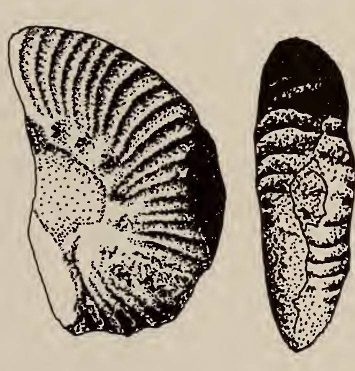

Fig. 9. *Olcostephanus* (*Olcostephanus*) cf. *atherstoni* (Sharpe). The holotype of *Taraisites bosei* Cantu Chapa, from the Taraises Formation of northern Mexico (after Böse 1923). × 1.

Cantu Chapa (1966) erected the genus *Taraisites* for the specimen of *Astieria* aff. *baini* Sharpe figured by Böse (1923: 76, pl. 2 (figs 3–5)) (Fig. 9 herein), renaming it *T. bosei* Cantu Chapa. This genus was characterized by distant secondary ribbing arising in bundles of 2–3 from the umbilical bullae. As remarked by Riccardi *et al.* (1971), Cantu Chapa's disregard for ontogenetic variation resulted in his separation of, amongst others, the small, coarsely ribbed paratypes of '*Rogersites*' *prorsiradiatus* Imlay, under the new species

name of *T. neoleonense*, from the larger and more densely ribbed holotype. Indeed, he included the type of *Olcostephanus baini* (Sharpe) within his new genus, thus separating a microconch from its far more densely ribbed macroconch dimorph. There can be no hesitation in following Riccardi *et al.* (1971) in considering *Taraisites* a synonym of *Olcostephanus* s.s.

Cantu Chapa (1966) also erected the new genus *Satoites* for the supposedly Berriasian *Olcostephanus* sp. nov. figured by Sato (1958: 590, pl. 28 (figs 1–3), fig. 2) (Fig. 10 herein), and considered ancestral to *Mexicanoceras* from which

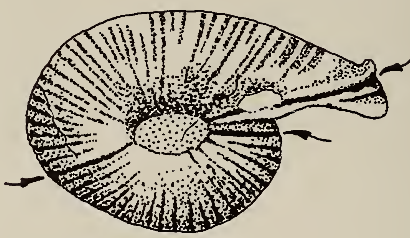

Fig. 10. *Olcostephanus oshimensis* (Cantu Chapa). The type species of the genus *Satoites*, allegedly from the Berriasian of Japan (after Sato 1958). × 1.

it was said to differ by the absence of a ventral furrow, whilst possessing prominent parabolae. Since the main criterion by which Imlay (1938: 562) distinguished *Mexicanoceras* from *Olcostephanus* was in the presence of a ventral furrow, *Satoites* must be considered a junior synonym of *Olcostephanus* s.s.

Thieuloy (1964: 212) erected the subgenus *Olcostephanus* (*Jeannoticeras*) for *Ammonites jeannoti* d'Orbigny (1840, pl. 56 (figs 3–5)) (Fig. 11 herein), characterized by the absence of umbilical tuberculation in the adult, and by the secondary ribbing which commonly arises in pairs (rarely three) from the primary ribs at the umbilical shoulder. Through C. W. Wright, the writer has seen a collection of *Olcostephanus* (*Parastieria*) from the Lower Hauterivian at Speeton. This subgenus is based upon a microconch species with lappets which upto the body chamber shows numerous primaries giving rise to fine secondaries in twos and threes. At this stage, *Parastieria* is indistinguishable from *Jeannoticeras* and it is only on the body chamber that the broad, flat ribs characteristic of *Parastieria* appear. Further work may show that *Jeannoticeras* is a junior subjective synonym of *Parastieria*, though for the time being they are treated as distinct.

The genus *Dobrodgeiceras* Nikolov (1962: 69) was established for the type species *D. ventrotuberculatum* Nikolov from the Upper Valanginian of Bulgaria, and said to differ from *Valanginites* mainly in the presence of ventral tubercles and more prominent primaries (Nikolov 1962: 69). Thieuloy & Gazay (1967) assigned their entire French fauna to *Dobrodgeiceras wilfridi* (Karakasch)

Fig. 11. *Olcostephanus* (*Jeannoticeras*) *jeannoti* (D'Orbigny), × 1. A–B. A specimen in the collections of the University of Paris from the Lower Hauterivian of Montclus, Hautes-Alpes. C. The crushed lectotype in the Natural History Museum, Paris, R3114 (D'Orbigny Collection No. 4865*a*) from the Lower Hauterivian of ?Serrais, Hautes-Alpes. Note the parabola.

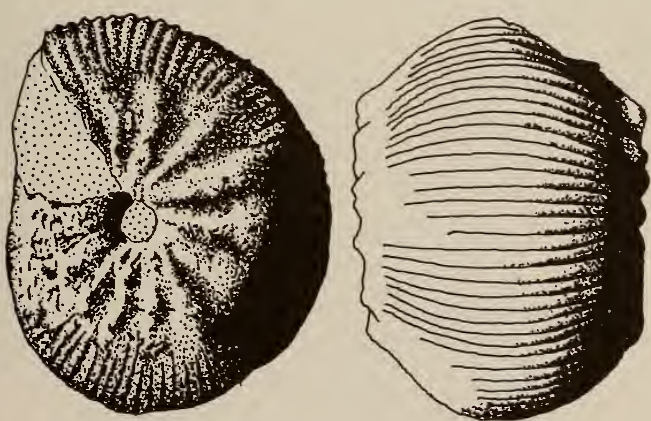

Fig. 12. *Dobrodgeiceras wilfridi* (Karakasch). The holotype of *Holcostephanus wilfridi* Karakasch from the Upper Valanginian of Crimea (after Karakasch 1902). × 1.

(Fig. 12) of which they considered *ventrotuberculatum* merely a subspecies. Riccardi & Westermann (1970) considered that the French sample was derived from a single population, and since '. . . the use of the subspecies category in palaeontology is usually confined to stratigraphically or geographically distinct taxa. . . . The interpretation of this variation as genetic polymorphism is

probably correct.' According to Riccardi & Westermann (1970), the position of the flank tubercles in *Dobrodgeiceras* is ventrolateral, and not lateral or periumbilical as described by Thieuloy & Gazay (1967: 77). The similarity with *Valanginites* led Riccardi & Westermann to place *Dobrodgeiceras* within the Polyptychitinae. However, since this subfamily is generally distinguished by the branching of the secondaries, a feature unknown in both *Valanginites* and *Dobrodgeiceras*, there appears no reason why they should not preferably be included within the Olcostephaninae.

Valanginites is a much misunderstood genus although the situation has recently been clarified somewhat by Thieuloy (1977*a*). Thus, a survey of the literature shows that at some time or other most strongly inflated, coarsely ribbed olcostephanids have been referred to this genus. Spath (1930) included *O. perinflatus* (Matheron) and *O. stephanophorus* (Matheron) in this genus, rectifying his mistake in 1939, but now including *O. crassus* (Zwierzycki) and, tentatively, *Holcostephanus bachelardi* Sayn into *Valanginites*. Imlay (1938) erected the species *Valanginites angusticoronatus* for a coarsely ribbed, inflated form which is herein considered to be an *Olcostephanus*, very close to *O. rogersi* (Kitchin) (♀). The only undoubted species of *Valanginites* appear to be the type species *V. nucleus* (Römer), of which *V. utriculus* (Matheron) was considered a synonym by Roch (1930), *V. dolioliformis* (Roch) (Fig. 13), *V. tijerensis* Imlay, *V. psaephoides* (Mayer–Eymar) (including *V. bachelardi* (Sayn)), and *V. simplus* (d'Orbigny). Of these, umbilical tubercles are present in *V. dolioliformis* and *V. tijerensis*.

Leanza (1957) described four species of the Hauterivian genus *Simbirskites* from the Upper Valanginian of Argentina. Rawson (1971: 42), however, considers this material generically misidentified since '. . . all four of Leanza's

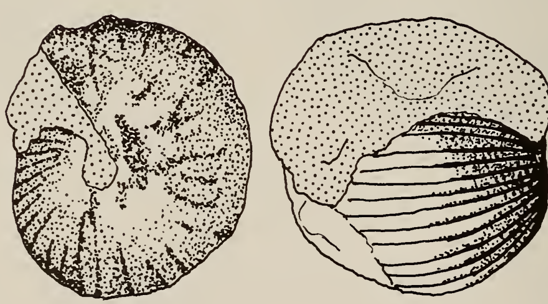

Fig. 13. *Valanginites dolioliformis* (Roch). The holotype from Morocco (after Roch 1930). × 1.

species differ from *Simbirskites* in that the ribs extend straight across the venter instead of curving forwards. Leanza's species appear closer to *Rogersites*; the recorded stratigraphical horizon (late Valanginian) would agree with this.'

The Argentinian material can immediately be precluded from the subgenera *Mexicanoceras*, *Jeannoticeras*, and *Parastieria*. They differ from *Olcostephanus* s.s. (= *Rogersites*) in having prorsiradiate primary ribs throughout ontogeny, in having a gently sloping umbilical wall and rounded umbilical shoulder throughout ontogeny, and in being more evolute. While any one, or even all, of these characters may be found at some growth stage in *Olcostephanus* s.s., they are not known to persist together throughout ontogeny. The sloping umbilical wall, coronate whorl section and prorsiradiate primaries of Leanza's *S. araucanus* are, however, all to be found in *Olcostephanus* (*Subastieria*) *nicklesi* Wiedmann & Dieni, and it is to this subgenus that the Argentinian material is best referred. The Argentinian material would seem to comprise some of the few adult examples of this subgenus yet recorded. In maturity, therefore, *Subastieria* should be regarded a close homoeomorph of *Simbirskites*; possibly the latter is descended from the former.

Thieuloy (1977*a*: 432) has recently introduced the new subgenus *Lemurostephanus* within *Olcostephanus* for forms with a very wide umbilicus (40–45% of the diameter), well-developed parabolae and primary ribs terminating in pointed bullae from which arise bundles of 2–4 secondary ribs. Besides the type species, *Holcostephanus madagascariensis* Lemoine (Fig. 14), Thieuloy (1977*a*)

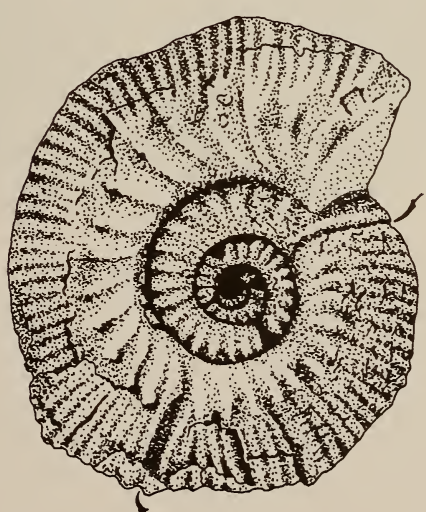

Fig. 14. *Olcostephanus* (*Olcostephanus*) *madagascariensis* (Lemoine). The holotype from the Lower Valanginian of Madagascar (after Collignon 1962). × 1.

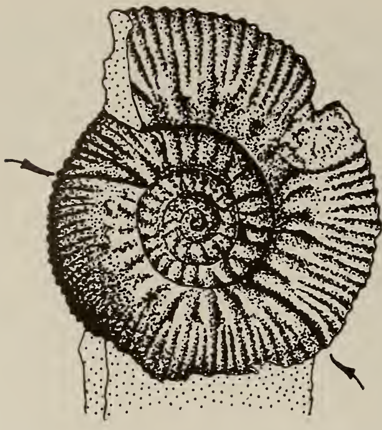

Fig. 15. *Olcostephanus* (*Olcostephanus*) *mitreanus* (d'Orbigny) (♂). The holotype of *Astieria detonii* Rodighiero from Venice (after Rodighiero 1919). × 1.

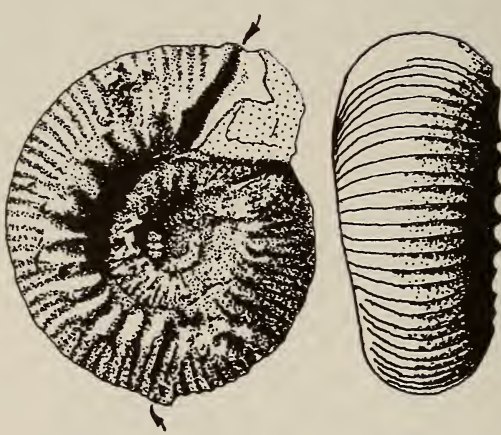

Fig. 16. *Olcostephanus* (*Olcostephanus*) *mitreanus* (d'Orbigny) (♂). The holotype of *Olcostephanus wynnei* Spath from the Spiti Shales of Pakistan (after Spath 1939). × 1.

also included in this subgenus *Spiticeras detonii* Rodighiero (Fig. 15), *Olcostephanus wynnei* Spath (Fig. 16), *Olcostephanus mitreanus* (d'Orbigny) (Fig. 17), *O. sanctifirminensis* Thieuloy, *Holcostephanus chaignoni* Sayn, *Maderia*? *latiumbilicata* Imlay and the species of '*Simbirskites*' described by Leanza (1957) and discussed above. Of these, Leanza's '*Simbirskites*' species together with *H. chaignoni* Sayn, *Maderia*? *latiumbilicata* and *O.* (*L.*) *sanctifirminensis* can adequately be included in the subgenus *Subastieria*, whilst *Spiticeras detonii*, *Olcostephanus wynnei* and *O. mitreanus* are conspecific microconchs whose

Fig. 17. *Olcostephanus* (*Olcostephanus*) *mitreanus* (d'Orbigny). The syntypes in the Natural History Museum, Paris, R3118 (D'Orbigny Collection No. 4871), of which the smaller (a microconch) has been selected as lectotype (Thieuloy 1977*a*). The paralectotype would seem to be an immature macroconch. × 1.

probable macroconch, *O. collignoni* (Besairie) (Fig. 18), is a typical *Olcostephanus* s.s. In the writer's opinion, the subgenus *Lemurostephanus* comprises an heterogeneous assemblage of *O.* (*Subastieria*) and *O.* (*Olcostephanus*) and is of little taxonomic significance. The author prefers not to use the name.

During the early ontogenetic stages (Fig. 19), the suture line of *Olcostephanus* is relatively simple with long, thin saddles and a trifid first lateral lobe (L). With ontogeny the suture becomes very deeply incised (Fig. 20K) with long, thin folioles and lobules. *Olcostephanus* (*Subastieria*) *hispanicus* (Mallada) (Fig. 20H–I) shows a similar suture line, as does *Dobrodgeiceras broggianum* (Lissón), although in the latter the saddles are broader and shorter (Fig. 20J).

The following subdivisions within the Olcostephaninae are here recognized:

S. (*Saynoceras*). Small, inflated microconchs with trapezoidal whorl sections.

Fig. 18. *Olcostephanus* (*Olcostephanus*) *collignoni* (Besairie) (♀). The holotype from the Upper Valanginian of Ambiky, Madagascar. × 1.

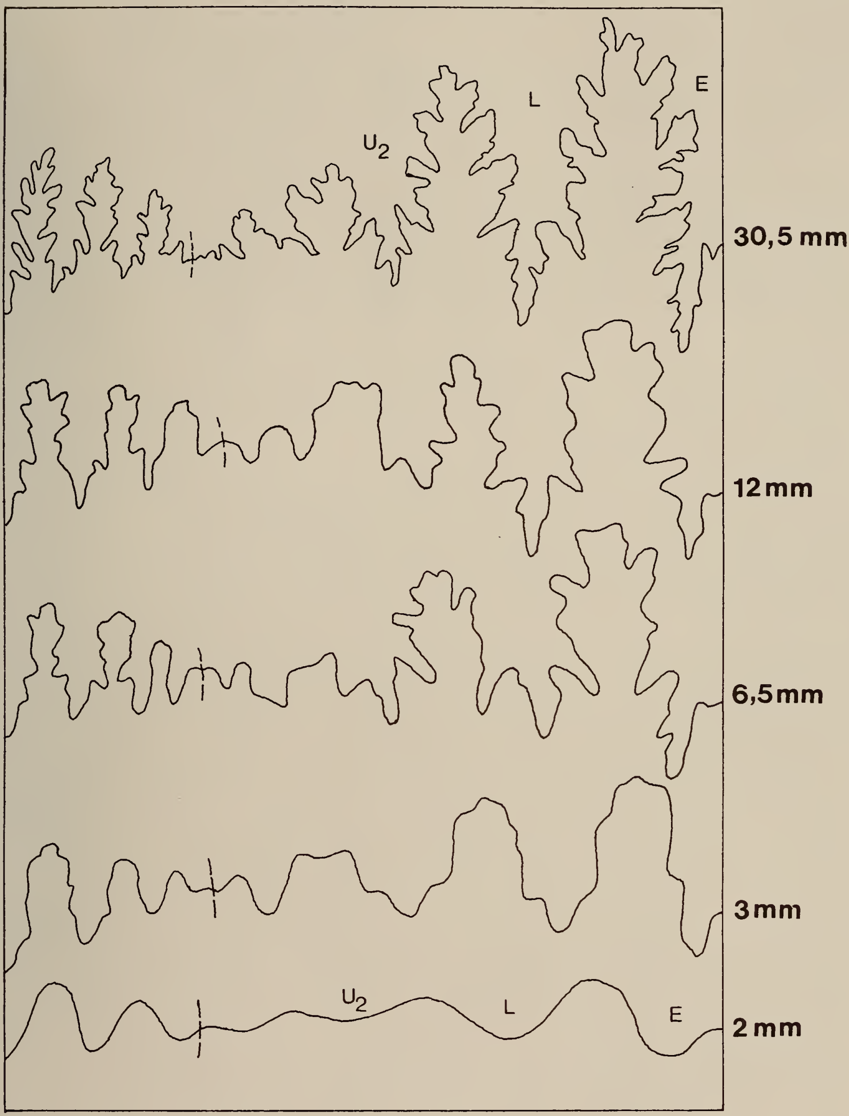

Fig. 19. Sutural ontogeny of *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♂) (after Riccardi *et al.* 1971).

Fig. 20. Olcostephaninid suture lines. A. *Olcostephanus* (*Olcostephanus*) *guebhardi* (Kilian) (after Baumberger 1908). B. *Olcostephanus* (*Olcostephanus*) *imbricatus* (Baumberger) (after Baumberger 1908). C. *Olcostephanus* (*Olcostephanus*) *leptoplanus* (Baumberger) (after Baumberger 1907). D. *Olcostephanus* (*Olcostephanus*) *ventricosus* (von Koenen) (after Tzankov 1943). E. *Olcostephanus* (*Olcostephanus*) *inordinatus* (Tzankov) (after Tzankov 1943). F. *Olcostephanus* (*Olcostephanus*) *inordinatus* (Tzankov) (after Pictet & Campiche 1860). G. *Valanginites bachelardi* (Sayn) (after Tzankov 1943). H,J. *Olcostephanus* (*Subastieria*) *hispanicus* (Mallada) (after Tzankov 1943). I. *Dobrodgeiceras broggianum* (Lísson) (after Riccardi & Westerman 1970). K. *Olcostephanus* (*Olcostephanus*) *baini* var. *sphaeroidalis* (Spath); drawn from the holotype, × 1.

Umbilical tubercles give rise to 1–2 weak ribs leading to ventrolateral tubercles; ribbing normally subordinate to tubercles on outer whorl, but may be sharp at some stages (after Wright *in* Arkell *et al.* 1957). Age: low Upper Valanginian.

S. (*Ceratotuberculus*). Small, inflated, like *Saynoceras*, but with more, 2–4, secondaries per tubercle, and with a smooth ventral furrow. Age: Lower Hauterivian.

O. (*Olcostephanus*). Compressed to inflated forms, usually with primary ribs terminating in tubercles on the umbilical shoulder, from which secondary ribs diverge in fasciculate bundles to pass uninterrupted across the venter. Parabolae may or may not be present. Dimorphic; males small, with lappets, females large and with simple peristomes. Age: Valanginian–Middle Hauterivian.

O. (*Subastieria*). Similar to *O.* (*Olcostephanus*), but with sloping umbilical wall, prorsiradiate primaries and a coronote whorl section throughout ontogeny. Adults homoeomorph *Simbirskites*. Age: Upper Valanginian–Lower Hauterivian.

O. (*Parastieria*). Based upon a lappeted microconch species. Inner whorls with numerous, fine primaries giving rise to 2–3 flexuous secondary ribs with intercalatories between bundles. Body chamber high-whorled, compressed, with slightly sinuous, broad, flat-topped ribs and no umbilical tubercles, Age: Lower Hauterivian.

O. (*Jeannoticeras*). Similar to *O.* (*Parastieria*) from which it is doubtfully separable, but with fine bundled ribbing retained on to the adult body chamber. Dimorphic. Age: Lower Hauterivian.

O. (*Mexicanoceras*). As for *O.* (*Olcostephanus*) but small, with ribs interrupted on outer whorls by a ventral furrow. Age: ?Lower Hauterivian.

Dobrogeiceras. Like *O.* (*Olcostephanus*) but very involute; umbilical tubercles have moved to the ventrolateral position, with a consequent lengthening of the prominent primary ribs. Ventral tubercles (?dimorphic) may be present on the body chamber. Age: Upper Valanginian.

Jeanthieuloyites. Similar to *Olcostephanus*, but with long, radial, nontuberculate primaries extending to mid-flank where they regularly bifurcate. Prominent, oblique parabolae. Age: Upper Valanginian.

Valanginites. Extremely inflated with very narrow umbilicus. Umbilical tubercles weak to absent. Secondary ribbing coarse, simple. Age: Upper Valanginian.

Capeloites. Small, compressed, with lappets (microconch). Inner whorls with prominent umbilical bullae from which pairs of ribs (the adoral one thick and robust and the adapical one fine and delicate) are looped to siphonal clavi. Intercalatories occur. On the body chamber siphonal clavi disappear, umbilical bullae weaken considerably, and all secondaries become fine, sinuous, passing uninterrupted across the venter. Age: Uppermost Valanginian–basal Hauterivian.

SEXUAL DIMORPHISM IN AMMONITES

It has long been noted that many ammonites occur in both large and small forms within the same stratum. Whereas the large forms have simple peristomes, the persitomes of the small forms frequently have various types of apertural adornment, e.g. lateral lappets, ventral rostra, ventral horns, etc. Furthermore, many such pairs were seen to have identical early whorls. This led to the concept of sexual dimorphism and, by analogy with extant invertebrates, the large forms were taken to represent the females and the smaller forms the males. Within recent years much attention has been given to the phenomenon of sexual dimorphism within fossil Cephalopoda (Callomon 1957, 1963; Makowski 1962*a*, 1962*b*; Westermann 1964, 1969; Houša 1965; Lehmann 1966, 1969; Palframann 1966, 1967; Cope 1967; Cobban 1969; Zacharov 1969; Reyment 1971; Riccardi *et al.* 1971; Kennedy & Cobban 1976), and it is now a widely accepted phenomenon.

It has often been noted, and Makowski (1962*a*) in his classical study placed much emphasis on the fact, that the inner whorls of the female are invariably identical to the male dimorph.

Douvillé (1880), in his study of *Morphoceras pseudoanceps*, noted that it had inner whorls identical to those of *M. polymorphus* and suggested that they possibly represented a dimorphic pair. Haug (1893) found that the inner whorls of *Sonninia sowerbyi* and *S. sulcata* were identical, and hence indistinguishable, up to a diameter of 30 mm, after which the later ontogenetic stages differed markedly. Makowski (1962*a*) has provided numerous examples from such widely diversified groups as the haploceratids, stephanoceratids, hildoceratids, cheiloceratids, and the scaphitids, where the inner whorls of the large macroconchs (♀) were identical to the smaller microconchs (♂). Palframann (1966) showed *Creniceras renggeri* (Oppel) and *Taramelliceras richei* (de Lorial) to be identical in every feature up to a diameter of about 8 mm. On the body chamber *T. richei* differed from *C. renggeri* in the development of ventrolateral spines. Furthermore, the peristome of *C. renggeri* was highly ornate, whereas that of *T. richei* was relatively simple. Palframann concluded that *C. renggeri* and *T. richei* were merely male and female of the same species. Similar identity of the early growth stages of *Distichoceras bicostatum* (Stahl) and *Horioceras baugieri* (d'Orbigny) led Palframann (1967) to consider them to represent a sexually dimorphic pair. Sutural approximation within a juvenile macroconch of *D. bicostatum* led Palframann (1967: 73) to suggest '. . . it may be that the specimen in question has changed sex during life as do some living molluscs. The latter explanation is considered unlikely though, as this feature has not been seen in other specimens studied here, the explanation of the phenomenon is itself, no doubt, unusual.'

Cope (1967), in a re-examination of the fauna of the Upper Kimmeridge Clay of Dorset, observed a unique type of dimorphism in the perisphinctid *Pectinatites*, in which the apertural ornament of the microconch is in the form of a ventral horn. As a general rule, he found that in this genus the microconch was usually slightly coarser ribbed than its macroconch at a similar diameter.

Riccardi *et al.* (1971) observed that identity of ornament between *Olcostephanus atherstoni* (Sharpe) dimorphs was restricted to the nucleus under 20 mm in diameter.

It is significant, however, that in all cases where there is identity of early ontogenetic stages in ammonites the change is always from a younger, typically male-type morphology to an older female-type morphology. According to Fretter & Graham (1964: 130) '. . . consecutive hermaphrodites change sex once in their lives, usually from a younger male to an older female phase', whilst Henderson & Henderson (1967: 478) define protandry as the '. . . condition of hermaphrodite plants and animals where male elements mature and are shed before female elements mature'.

A necessary prerequisite for the hypothesis of protandrism is, therefore, that the forms involved are simultaneous hermaphrodites. To prove this it would be necessary to study the soft parts of an ammonite, an obvious impossibility.

Whilst hermaphroditism is virtually unknown among extant Cephalopoda, having been recorded from but a single specimen of *Octopus vulgaris* (Pickford 1947: 522), it is known to occur in many species of Bivalvia and Gastropoda. Indeed, a tendency towards protandrism is frequent in many simultaneous hermaphrodites. Amongst the Bivalvia simultaneous hermaphroditism is known in *Pecten*, *Chlamys*, *Cardium*, *Teredo*, *Poromya*, etc. Not all species of these genera are, however, hermaphroditic. Thus *Cardium edule* is dioecious; whilst in some simultaneous hermaphrodites, e.g. *Teredo diegensis*, a certain number of young males never change sex and must therefore be regarded as true males.

In the Gastropoda simultaneous hermaphroditism is well known amongst the opisthobranchs and the pulmonates, as well as occurring to a limited extent in the prosobranchs, e.g. *Diodora*, *Puncturella*, *Patella*, etc. Whilst *Diodora* is predominantly dioecious, Bacci (1947) has shown about 12 per cent to be protandrous hermaphrodites. Orton (1920) claimed that 90 per cent of a population of *Patella vulgata* changed sex from male to female. Orton *et al.* (1956) found small specimens of *P. vulgata* (16–25 mm shell length) to be 90 per cent males; those with shells 40 mm long were male and female in equal proportions, whilst those with a shell length of 60 mm were 60–70 per cent females. With the exception of the well-known protandrous hermaphroditism of *Crepidula* (Coe 1936), little is known of the conditions in the other hermaphroditic prosobranchs, beyond the fact that most seem to be protandrous consecutive hermaphrodites.

It can be seen, therefore, that protandrous hermaphroditism, and consequently also simultaneous hermaphroditism, are well known in the other molluscan classes and it seems possible that it was at some stage equally common in the Cephalopoda. The fact that extant cephalopods are dioecious is not, therefore, in itself significant since, according to Fretter & Graham (1964: 128), '. . . there is some evidence for regarding the hermaphroditic state as the primitive one, especially in the phylum Mollusca'.

When the literature on sexual dimorphism in ammonites is studied, it is found that the occurrence of rare, aberrant mutants supports the possibility that some ammonites were, in fact, hermaphroditic.

Makowski (1962*a*: 23) considers the genus *Hecticoceras* to exhibit type 'A' dimorphism, i.e. microconchs have 5–6 whorls and macroconchs at least 7, with a morphological hiatus of one whorl between the two dimorphs. However, of the 21 specimens studied, Makowski noted that 3 examples had '. . . 6½ whorls each, their aperture is not quite simple, but is nearing that of the growth stages of large forms and provided with small broad lappets. However, the spiral pattern followed is that of large forms, completely different from the spiral in the small forms. Hence, they should be regarded as large forms whose growth halted at the stage with about 6½ whorls.' Makowski (1962*a*) makes no mention of whether he is dealing with a single species, and thus the true value of the observation is lost. If, however, the *Hecticoceras* in question were all referable to a single species, then this combination of male (lappets) and female (spiral form) characteristics would seem to suggest hermaphroditism.

Cope (1967: 53) recorded 4 specimens of *Pectinatites* (*Virgatosphinctoides*) *reisiformis densicostatus* Cope which he considered to be 'intersexual'. Thus, '. . . one specimen is intermediate in size between macroconch and microconch and has rib density of a typical microconch up to a diameter of 30 mm. Thereafter it becomes more finely ribbed, and is intermediate between macroconch and microconch in rib density'.

'At a diameter of 94 mm a horn is developed, and beyond this there is about three-eighths of a whorl of coarsely ribbed shell with sculpture similar to the outer whorls of a macroconch, but bearing four further horns . . . in addition to the above specimen which is absolutely intermediate in character between macroconch and microconch, three other specimens show a slight degree of intersexuality. These three specimens are apparently normal macroconchs to judge by their size, rib density and sculpture. They do, however, develop a type of horn in the later stages of development; this appears at a diameter of 140–150 mm and is unlike the true microconch horn in that it is developed from a single rib, has negligible ventral projection but projects laterally some distance down the whorl side. In addition, the diameter at which these structures are developed is much greater than that at which the true horn of the microconch occurs.'

Whilst the intermediate size of the mutants described by Cope (1967) need not necessarily be significant in view of the possible size overlap between dimorphs, as was noted by Cobban (1969: 9) in his study of *Scaphites leei* and *S. hippocrepis*, the typical female-type ribbing, associated with male-type ornament is, and must surely be, interpreted not as intersexuality but rather as bisexuality.

It is suggested that these rare observations of apparent bisexuality, and thus hermaphroditism, support the evidence provided by the shells of sexually dimorphic ammonites that some ammonites changed sex from a younger male phase to an older female state, and thus provide the first examples of protandrism

within the class Cephalopoda. It should be noted, however, that by analogy with extant Mollusca, not all species of even a single genus need be protandrous, nor even hermaphroditic.

Little is known of the exact reasons for protandric changes within those molluscs which are simultantous hermaphrodites. Pellegrini (1948), in his study of *Patella coerulea*, concluded that the change of sex was restricted to the resting period between successive breeding seasons and liable to affect animals of any age. Fretter & Graham (1964) consider the change to take place in such a way as to render the animals one sex early in the breeding season, and of the other sex later, or there may have been a winter pause between the two phases. According to Barnes (1968: 309) the sex of the older individuals is influenced at least partly by the presence or absence of other sexes in teh association. Thus, in *Crepidula* '. . . young specimens are always males. This initial male phase is followed by a period of transition in which the male reproductive tract degenerates; the animal now develops into a female or another male. . . . An older male will remain male as long as it is attached to a female. If such a male is removed or isolated it will develop into a female. The presence of a large number of males influences certain of the males to become females. When the individual once becomes female, it remains in that state.'

The work of Gould (1919, 1947) and Coe (1938*a*, 1938*b*, 1944, 1948) suggests that the transition from male to female occurs at different times in different individuals, indicating sex changes to be influenced by other animals in the chain, and by external stimuli.

When immature limpets are cultured in association with mature females, the great majority assume the functional male phase. Gould (1919, 1952) presented evidence, later supported by Coe (1953), to show that the formation and maintenance of the male phase is influenced by a substance or substances secreted in the water by mature females. Not all young males react in the same way to the mating stimulus.

SEXUAL DIMORPHISM IN *OLCOSTEPHANUS*

Within the Uitenhage olcostephanid fauna, sexual dimorphism is very apparent due to the unusually large size attained by the macroconch forms, some of which exceed 300 mm in diameter, whereas the largest undoubted microconch so far recorded from these beds is only slightly more than 100 mm in diameter, with the average far less. As recognized within many of the European Jurassic faunas, there are two distinct size groups (Fig. 21)—small forms with lappets and large forms with simple peristomes. However, these two distinct size groups comprise three morphological components (see Figs 22–23). There are small forms, both with and without parabolae, which bear lateral lappets and represent microconchs; there are moderately large strongly inflated forms, falling both into the microconch and macroconch size groups, both with and without parabolae and invariably without the peristome preserved; and,

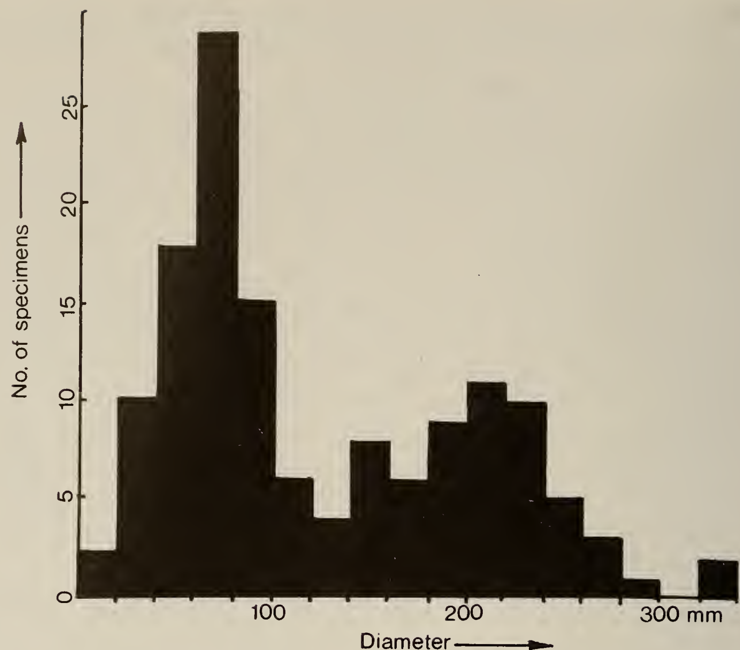

Fig. 21. Size-frequency histogram of the Uitenhage *Olcostephanus* fauna, showing the double peak corresponding to microconch and macroconch dimorphs.

finally, there are gigantic, generally strongly inflated forms lacking parabolae and with simple peristomes representing mature macroconchs. The intermediate groups have one feature in common; they are all inflated beyond the limits of microconchs and hence must be considered immature macroconchs. However, many of them differ from mature macroconchs in possessing parabolae, features which never occur on the outer whorls, except in the form of the simple peristome, of mature female forms. That some macroconchs had parabolae on their earliest whorls is revealed by a gigantic phragmocone of *O. rogersi* (Kitchin) (Fig. 71A–D), corresponding to a diameter of approximately 200 mm, which shows the impression on an inner whorl, corresponding to a diameter of about 60 mm, of a prominent parabola. Parabolae would seem, therefore, to be restricted to the inner whorls of certain macroconchs, and to certain microconchs. Whether parabolae are the product of male genetic control alone, thereby providing evidence of protandry in *Olcostephanus*, is uncertain in view of the slight but significant morphological differences between the inner whorls of macroconch forms and the microconch dimorph beyond a diameter of 20 mm. As concerns *O. baini* (Sharpe) dimorphs, the macroconch is already distinguishable at 30 mm diameter from the microconch by its slightly more numerous secondaries, with invariably 3 secondaries per bulla as against the 2–3 of the microconch. This is in accord with the observations of Cope (1967) on dimor-

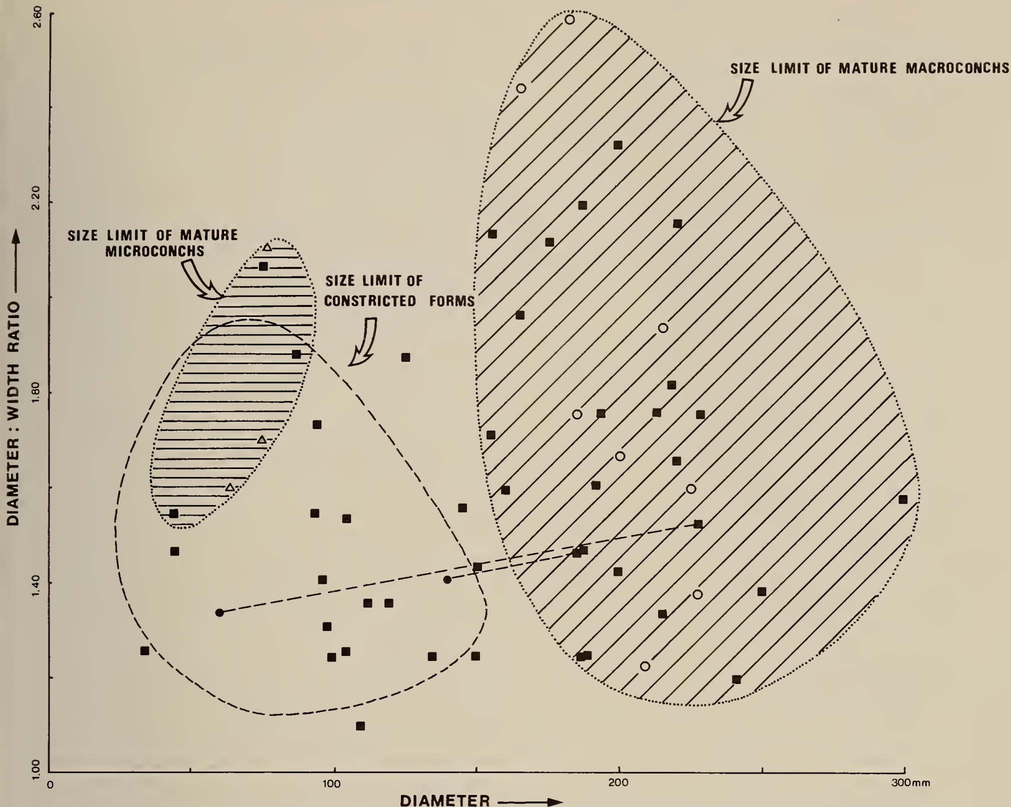

Fig. 22. Diameter/inflation plot for the unconstricted individuals of *Olcostephanus* from the Sundays River Formation. Squares = unconstricted forms; open triangles = unconstricted forms with lappets; circles = unconstricted forms with simple peristome.

phism in the Upper Jurassic genus *Pectinatites*, and also those of Riccardi *et al.* (1971) on *Olcostephanus*, that the inner whorls of the macroconch forms tend to be slightly more densely ribbed than the microconch dimorph.

The largest diameter at which parabolae have been observed is approximately 120 mm diameter, whilst an immature macroconch of *O. baini* (Sharpe), recognizable by its denser ribbing, shows a noticeable increase in inflation immediately after a parabola at 60 mm diameter (Fig. 151B–D).

Within the Uitenhage fauna there is no size overlap between corresponding macroconchs and microconchs.

THE PERISTOME IN *OLCOSTEPHANUS*

The commonest modification to the microconch aperture is the development of lateral lappets although, as already noted, in some ammonites this takes the form of a rostrum, a ventral lappet, or a ventral horn.

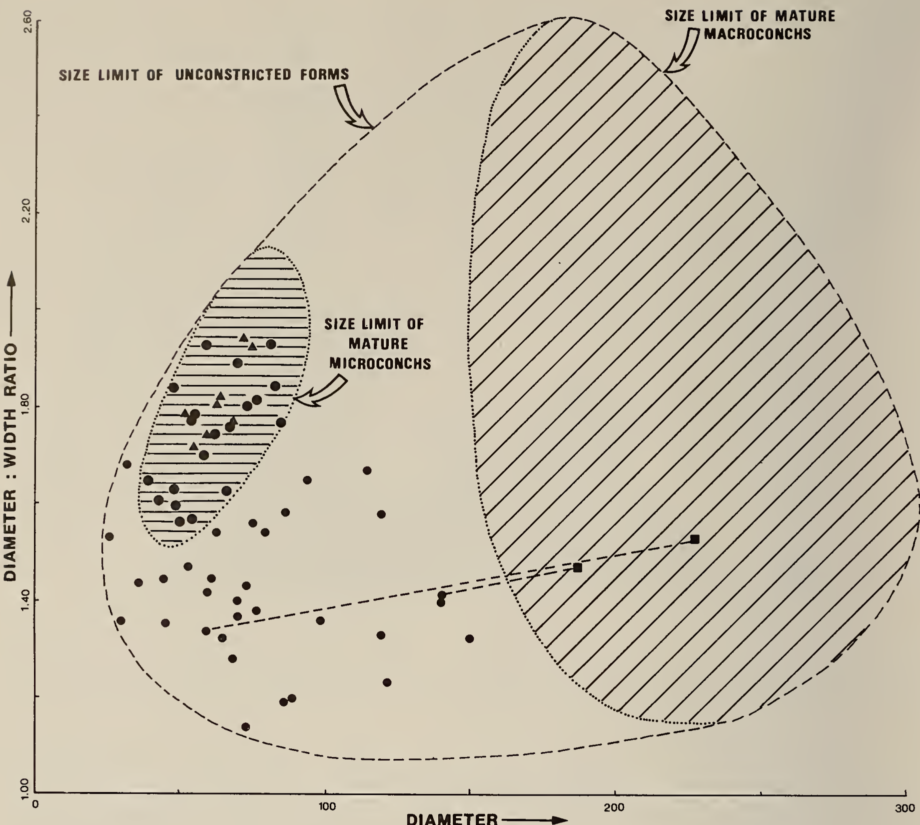

Fig. 23. Diameter/inflation plot for the constricted individuals of *Olcostephanus* from the Sundays River Formation. Dots = constricted forms; closed triangles = constricted forms with lappets.

The function of these apertural extensions has long been a subject of contention. Thus, Cope (1967: 17) considered the ventral horn in *Pectinatites* to possibly have assisted in copulation by housing the spadix. According to Bidder (*in* Westermann 1971), however, such a horn was more likely a median glandular modification equivalent to Van der Hoeven's organ. Lappets have even been compared with the claspers of insects, but according to Arkell (*in* Arkell *et al.* 1957: L92) '. . . their only conceivable function seems to be protective. In planulate and sphaerocone shells Westermann (1954) has noted that the microconchs frequently have exceptionally large, converging, lateral lappets, which caused the aperture to become occluded. According to Westermann (1971) such '. . . occluded apertures are obviously "specialized" features preventing macrophagous predation'. None the less, he was led to conclude that '. . . the function of the diverse apertural shapes, however, remains unknown'. It seems

to the writer most reasonable to interpret them as display characters, designed to attract females.

Lateral lappets are preserved in a number of examples of *Olcostephanus* from the Uitenhage Group, usually as internal moulds, although in a single specimen (Fig. 131A–B) the peristome is preserved as recrystallized test. In this microconch the peristome comprises a deep, slightly flexuous constriction, bordered adapically and adorally by prominent parabolic ribs. The adapical rib is prominently flared, whilst the adoral rib is associated with well-developed lateral lappets. On this same specimen, SAM–PCU1527, the outer whorl is seen to bear a parabola which takes the form of a prominent, deep, oblique constriction bordered by strongly developed parabolic ribs, the adapical rib being more strongly flared than that to the anterior. The parabola truncates ribbing adapically, but is parallel to the adoral ribbing. That such parabolae are associated with halts in growth is evidenced by the change in ribbing direction adorally, and often by a distinct change in inflation immediately after such a feature. Such parabolae are thus virtually identical to the peristome and must surely have an identical mode of formation. However, according to Arkell (*in* Arkell *et al.* 1957: L93) '. . . they [parabolae] are not, however, the same as the peristome of the adult shell, for often no such constriction or other features may be found at the end of the adult body chamber'. In *Olcostephanus* this is never the case, and it seems inconceivable that they owe their origins to two unrelated processes. Consequently, parabolae in *Olcostephanus*, at least, are interpreted as relict peristomes.

Accepting parabolae in *Olcostephanus* to represent relict peristomes, it is of interest to note that in many extant gastropods, e.g. *Charonia tritonis tritonis* (Linnaeus), the whorls are ornamented with varices which represent the position of relict apertures developed during halts in growth. They would appear, therefore, to be absolutely analogous to the parabolae occurring in *Olcostephanus*. What is especially interesting is the fact that in extant Gastropoda they are known to be of specific importance.

HOMOEOMORPHY IN *OLCOSTEPHANUS*

A significant feature associated with sexual dimorphism in *Olcostephanus* is a striking degree of convergence in the outer whorls of macroconch forms. This was already noted by Makowski (1962*a*: 21) who wrote '. . . we may note the side by side existence of large forms (macroconchs) whose last whorls and particularly the last body chamber are identical, while their young forms differ in section or in character of ornamentation. These differences, being not very striking, are not taken into account in the specific delimitation of large forms (macroconchs), they are, however, very readily discernible in small forms (microconchs) which repeat the character of the young whorls of large forms (macroconchs).'

It was this pitfall that led Riccardi *et al.* (1971) to regard *O. schenki* (Oppel)

(= *O. baini* ♀), a species with prominent parabolae, as merely the inner whorls of the large *O. atherstoni* macroconch, whilst their microconch forms of *O. atherstoni*, viz. *O. psilostomus* Neumayr & Uhlig, *O. wilmanae* (Kitchin), and *O. midas* (Leanza), do not possess such features.

With regard to convergence within macroconch forms of *Olcostephanus*, Spath (1930: 143) noted that '. . . examples like those figured by Burckhardt or by Böse from Mexico as *Astieria* cfr. *atherstoni* and *A.* ex. aff. *atherstoni* represent the outer whorls of *Olcostephanus* of the *astierianus–filosus* group such as are common in the south of France' and that '. . . it is probable that in each area that had its *Olcostephanus* fauna there were developed "*atherstoni*" forms which thus do not constitute a true species but are merely homoeomorphous local variants of the common root-stock' (Spath 1930: 34).

This convergence is very evident in the macroconch forms of the Uitenhage olcostephanid fauna. Thus, the macroconch forms of *O. atherstoni* (Sharpe) and *O. baini* (Sharpe) differ only in degree of inflation, whilst with a broad specific interpretation it would be possible to group most *Olcostephanus* macroconchs within a single species. By far the most important factor in the matching of sexual dimorphs is a close similarity between the inner whorls of the macroconch and the microconch dimorph. In those forms studied by Makowski (1962*a*) there was complete identity. In *Olcostephanus*, however, as noted by Riccardi *et al.* (1971: 96), identity of ornament is restricted to the nucleus under 20 mm diameter, with the inner whorls of the *O. baini* macroconch being slightly more densely ribbed at 30 mm diameter than the microconch at 50 mm diameter.

The fact that three morphological types, i.e. the microconch, the macroconch, and the inner whorls of the macroconch, may be distinguished within a single species has led to a proliferation of names, the majority endemic, which together with an almost complete disregard for intraspecific variation has led to taxonomic confusion.

DESCRIPTION OF THE SUNDAYS RIVER SPECIES OF *OLCOSTEPHANUS*

Olcostephanus (*Olcostephanus*) *atherstoni* (Sharpe, 1856)

Figs 9, 19, 24–26, 27A–D, 28–43, 55, 118, 143C–D, 151A

Microconch (♂)

Ammonites astieri Pictet & Campiche (*non* d'Orbigny), 1860: 298, pl. 43 (figs 1, 3 only).
Olcostephanus psilostomus Neumayr & Uhlig, 1881: 149, pl. 32 (fig. 2).
Astieria aff. *psilostoma* (Neumayr & Uhlig) von Koenen, 1902: 151, pl. 54 (fig. 21).
Astieria psilostoma (Neumayr & Uhlig) von Koenen, 1902: 151. Baumberger, 1907: 35, pl. 24 (fig. 6), pl. 21 (fig. 4), figs 111–113.
Astieria atherstoni (Sharpe) Baumberger, 1907: 39, pl. 21 (fig. 3), pl. 24 (figs 2, 5 only).
Astieria leptoplana Baumberger, 1908: 9, pl. 28 (fig. 2 only).
Holcostephanus wilmanae Kitchin, 1908: 195, pl. 9 (fig. 1).
Holcostephanus (*Astieria*) *psilostomus* (Neumayr & Uhlig) Wegner, 1909: 85.
Holcostephanus (*Astieria*) *psilostomus* var. *picteti* Wegner, 1909: 85.
Holcostephanus (*Astieria*) *psilostomus* var. *wilmanae* Kitchin, Wegner, 1909: 86.
Holcostephanus (*Astieria*) *psilostomus* var. *koeneni* Wegner, 1909: 86.

Fig. 24. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♀). Lateral view of the holotype, BM–C32202, × 1. Photo W. J. Kennedy.

Fig. 25. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♀). Ventral view of the holotype, BM–C32202. × 1. Photo W. J. Kennedy.

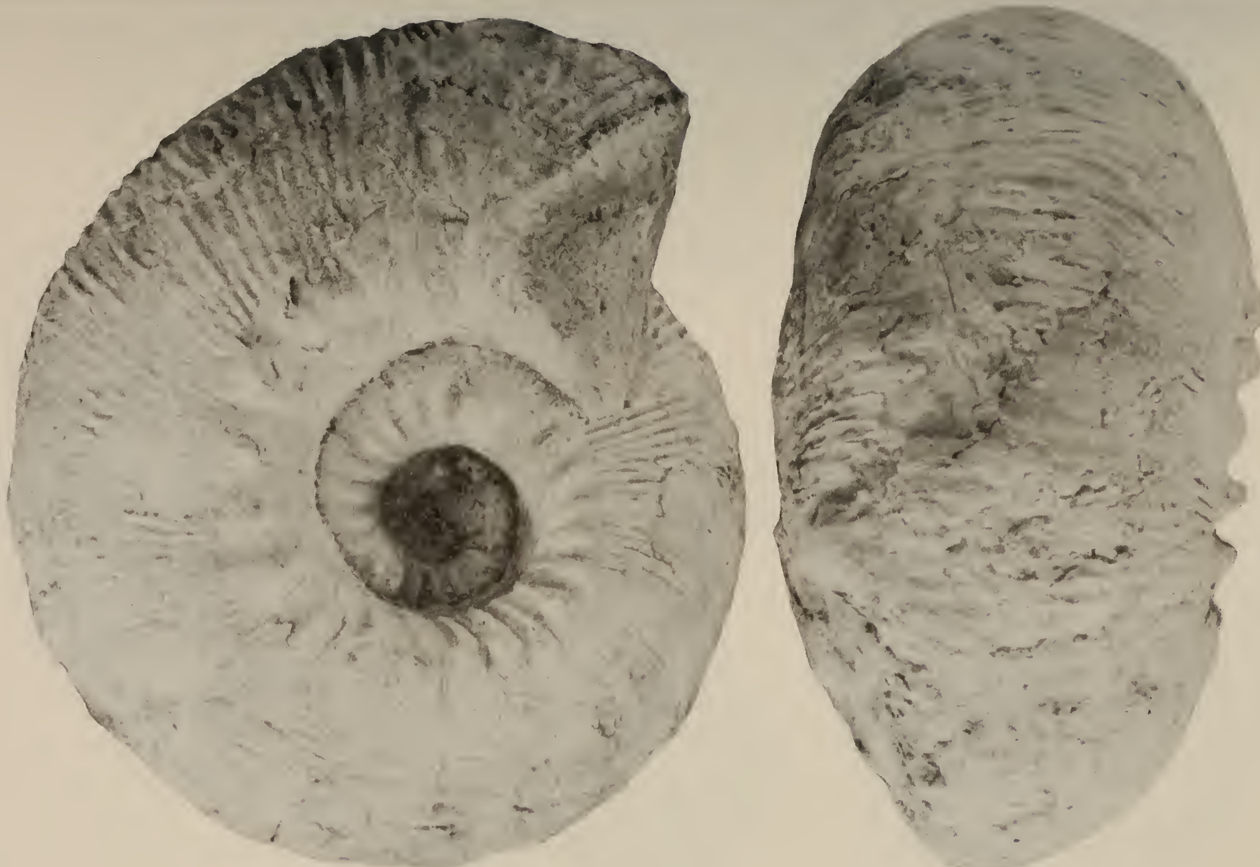

Fig. 26. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♀). Lateral and ventral views of BM–C47128. Note constant rate of inflation and constricted peristome. × 0,44.

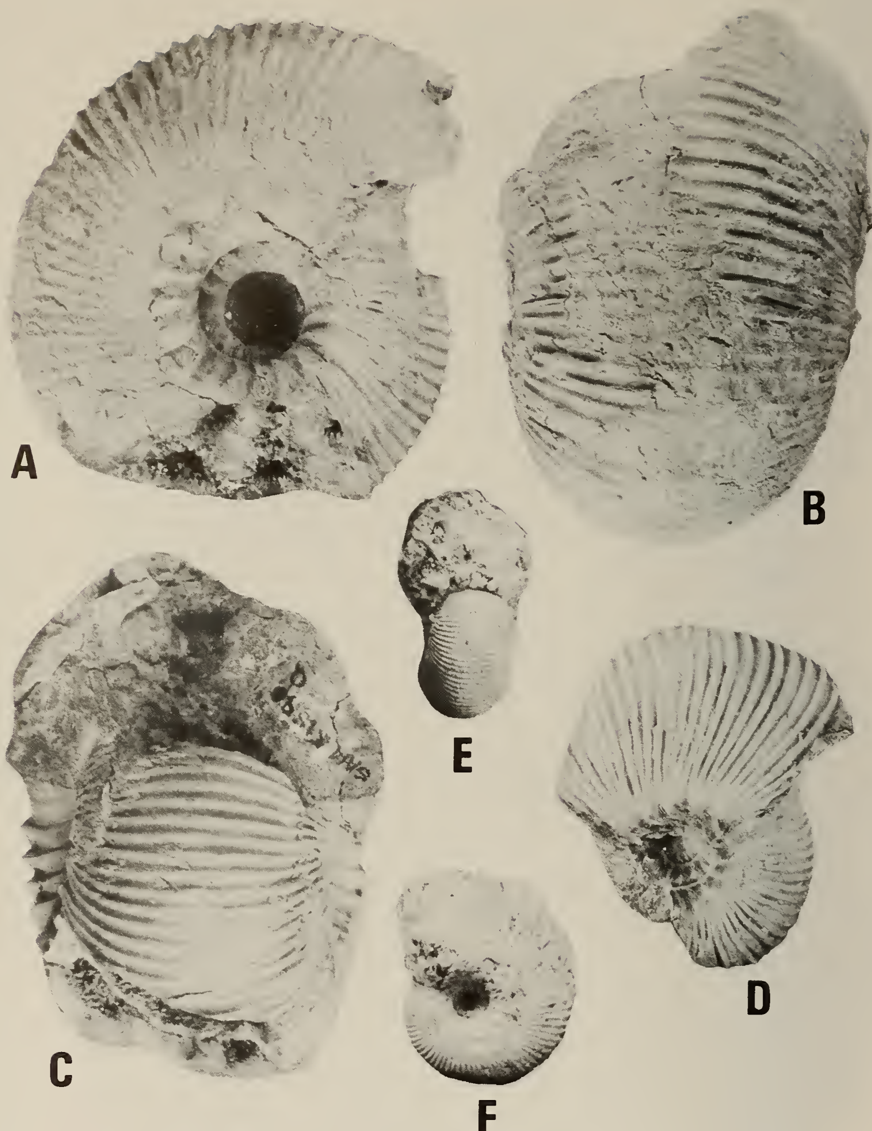

Fig. 27. A–C. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♀), × 0,66. Lateral, ventral and front views of SAM–PCU1590. D. Lateral view of a slightly crushed specimen. SAM–PCU1585. E–F. *Olcostephanus* (*Olcostephanus*) ?*densicostatus* (Wegner) sp. juv. Front and lateral views of SAM–PCU1612, × 1.

Fig. 28. *Olcostephanus* (*Olcostephanus*) cf. *atherstoni* (Sharpe) (♀). Lateral and ventral views of SAM-315. × 0,44.

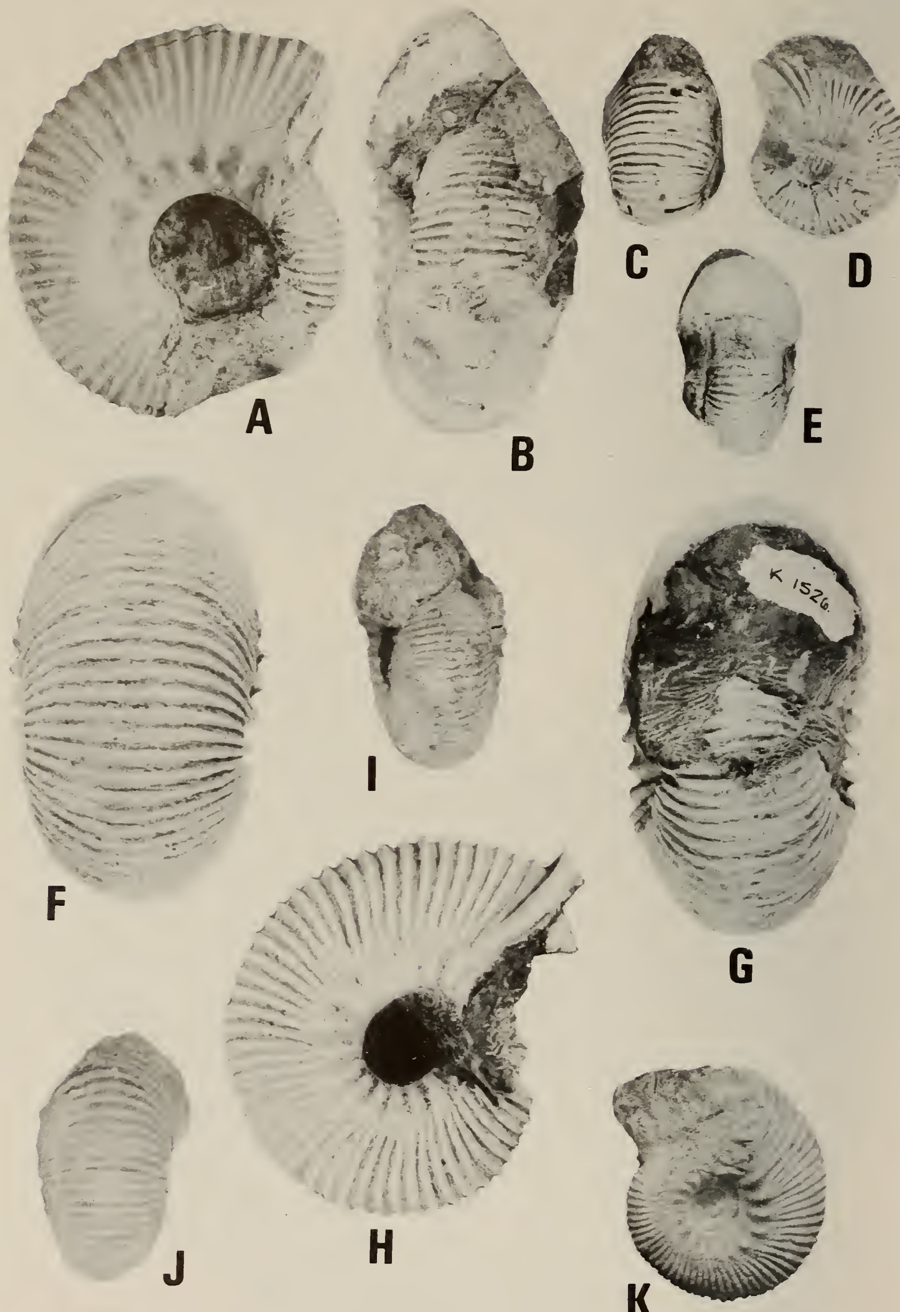

Fig. 29. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe). A–B. Lateral and front views of SAM–PCU1532, a microconch, × 0,75. C–E. Ventral, lateral and front views of SAM–PCU1608, a juvenile, × 0,66 F–H. Ventral, lateral and front views of SAM–PCU1526, a microconch, × 0,66. I–K. Front, ventral and lateral views of AM–839, a juvenile, × 0,68.

Fig. 30. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♂). The holotype of *Rogersites otoitoides* Spath, SAM–9242. × 0,75.

Astieria psilostoma var. *veneto* Rodighiero, 1919: 88, pl. 9 (fig. 11).
? *Astieria* aff. *baini* (Sharpe) Böse, 1923: 76, pl. 2 (figs 3–5).
Astieria psilostoma var. *crassa* Roch, 1930: 315.
Astieria psilostoma var. *lateumbilicata* Roch, 1930: 314, pl. 16 (fig. 3).
Rogersites otoitoides Spath, 1930: 149, pl. 14 (fig. 1).
Rogersites wilmanae (Kitchin) Spath, 1930: 145, pl. 13 (fig. 3), pl. 14 (fig. 4), pl. 15 (fig. 2).
Rogersites tenuicostatus Imlay, 1937: 562, pl. 73 (figs 3–9).
Holcostephanus midas Leanza, 1944: 16, pl. 1 (fig. 1).
? *Taraisites bosei* Cantu Chapa, 1966: 16.
Taraisites tenuicostatus (Imlay) Cantu Chapa, 1966: 16.
Olcostephanus atherstoni (Sharpe) (♂), Riccardi *et al.*, 1971: 91, pl. 12 (fig. 4), pl. 13 (figs 2–3).

Macroconch (♀)

Ammonites atherstoni Sharpe, 1856: 196, pl. 23 (fig. 1).
Olcostephanus atherstoni (Sharpe) Holub & Neumayr, 1882: 272. Riccardi *et al.*, 1971: 91, pl. 12 (fig. 3), pl. 13 (figs 1, 4 only).
Non Olcostephanus (*Astieria*) *atherstoni* (Sharpe) Pavlow & Lamplugh, 1892: 495 (= *O.* (*Subastieria*) *decipiens* Spath).
Holcostephanus (*Astieria*) *atherstoni* (Sharpe) Kilian & Leerhardt, 1895: 973. Wegner, 1909: 81. Kilian, 1910: 213.
Non Holcostephanus (*Astieria*) *atherstoni* (Sharpe) Kilian, 1902: 865, pl. 57 (fig. 1) (= ? *O. ventricosus* (von Koenen)).
Holcostephanus atherstoni (Sharpe) Uhlig, 1903: 132. Kitchin, 1908: 185. Collignon, 1962: 38, pl. 188 (fig. 860).
Non Holcostephanus (*Astieria*) cf. *atherstoni* (Sharpe) Karakasch, 1902: 103, pl. 1 (fig. 3) (= *O. sharpei* Karakasch).
Non Holcostephanus atherstoni (Sharpe) Hatch & Corstorphine, 1909: 303, fig. 76a (= *O. baini* (Sharpe)).
? *Astieria* cf. *atherstoni* (Sharpe) Baumberger, 1907: 39, pl. 23 (fig. 1), fig. 114 only.
Non Holcostephanus cf. *atherstoni* (Sharpe) Kitchin, 1908: 193 (= *O. baini* (Sharpe)).

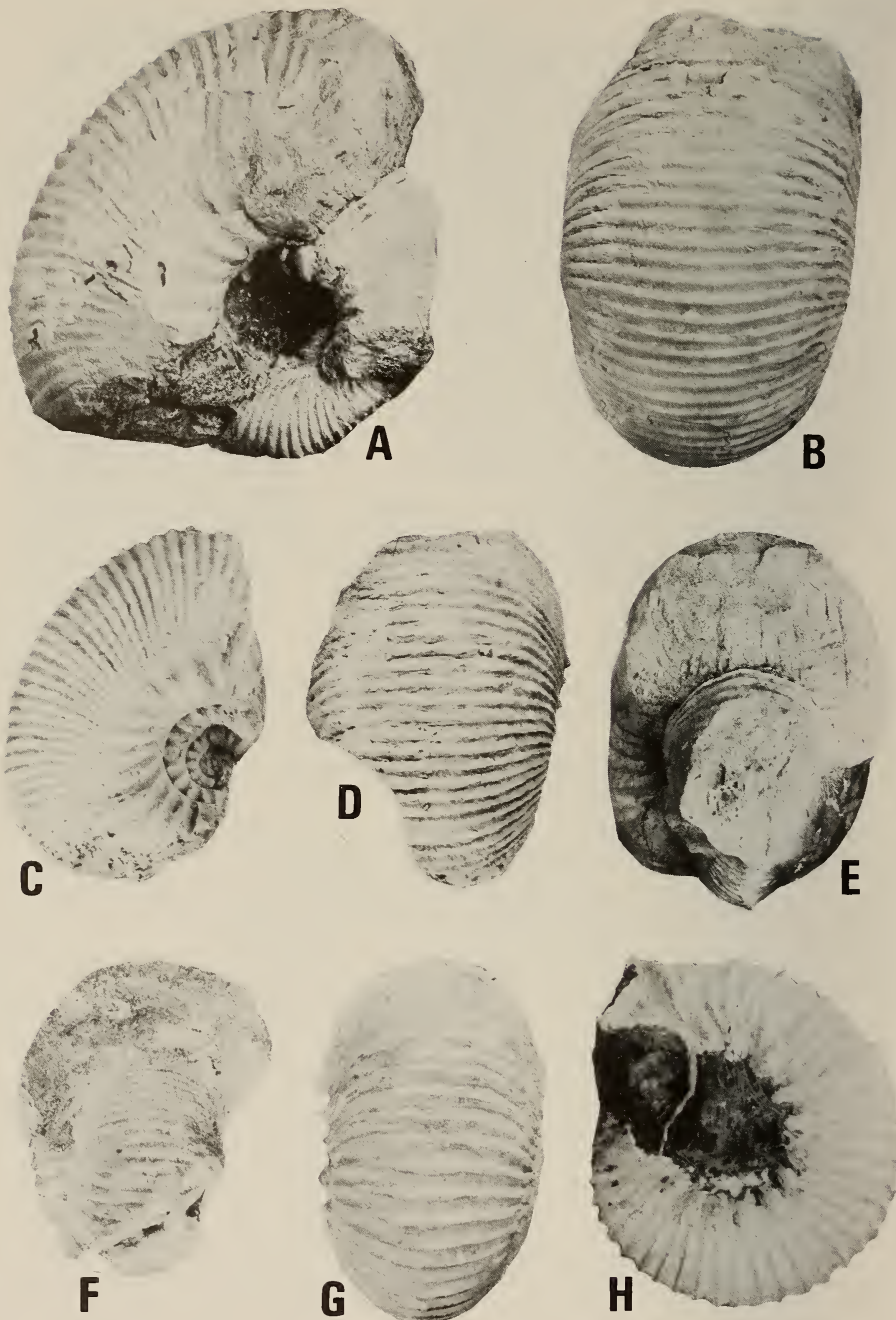

Fig. 31. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe). A–B, E. Lateral, ventral and front views of an immature macroconch, AM–4292, × 0,75. C–D, F. Lateral, ventral and front views of an immature macroconch, SAM–PCU1589, × 0,44. G–H. Ventral and lateral views of SAM–PCU1529, a microconch, × 0,66.

Astieria cf. *atherstoni* (Sharpe) Böse, 1923: 77, pl. 3 (figs 1–2).
Rogersites curvicostatus Besairie, 1936: 141, pl. 12 (figs 7, 10), pl. 13 (fig. 8).
? *Astieria* aff. *atherstoni* (Sharpe) Riedel, 1938: 13, pl. 3 (figs 5–6), pl. 12 (fig. 3).
Rogersites prorsiradiatus Imlay, 1937: 561, pl. 17 (figs 1–7).
Taraisites neoleonense Cantu Chapa, 1966: 16.
Olcostephanus (*Rogersites*) *atherstoni* (Sharpe) Spath, 1939: 32, pl. 20 (fig. 4).
? *Non Olcostephanus* (*Rogersites*) cf. *atherstoni* (Sharpe) Spath, 1939: 32, pl. 20 (fig. 3) (= ? *O. baini* (Sharpe)).
Rogersites atherstoni (Sharpe) Tzankov, 1943: 196, pl. 8 (figs 1–2, 4 only).
Non Olcostephanus cf. *O. atherstoni* Baumberger (*non* Sharpe), Imlay & Jones, 1970: B38, pl. 9 (figs 1–3, 6–10).

Material

18 specimens; 8 microconchs (SAM–PCU1526, 1529, SAM–9242, BM–C32199, 32204), 7 macroconchs (SAM–PCU1585, 1589–90, 1604, AM–4292, BM–C32202, 47128), and 3 juveniles (SAM–PCU1608, AM–839, 4293).

Holotype

By monotypy, the original of the specimen of *Ammonites atherstoni* figured by Sharpe (1856: 196, pl. 21 (fig. 1)) from the Sundays River, now in the British Museum, BM–C32202.

Diagnosis

Dimorphic. Microconch fairly small (60–100 mm in diameter), with peristome bearing lateral lappets. Primary ribs rursiradiate, terminating in about 18 bullae on the final whorl from which arise bundles of 3 prorsiradiate

Fig. 32. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♂). The holotype of *Holcostephanus wilmanae* Kitchin, BM–C32199, a laterally crushed microconch. × 0,75.

secondaries. There are 25–37 ribs per half-whorl. Parabolae lacking. Whorl section apparently variable. Macroconch large (+ 200 mm in diameter), strongly inflated, with well-rounded venter and depressed, semicircular whorl section. Primary ribs rursiradiate, terminating in 17–25 bullae at the umbilical shoulder from which arise bundles of 3–4 secondaries, with 1–2 intercalatories between bundles. There are 40–50 secondary ribs per half whorl. Parabolae absent at all growth stages. Peristome simple.

Description

Microconch (♂): the shell is rather small, with lappets present at diameters from 60–100 mm, and comprises somewhat inflated to rather compressed cadicones, involute up to the umbilical bullae so that about 75 per cent of the previous whorl is covered. The shell becomes slightly more evolute as the umbilical seam egresses on the adoral portion of the body chamber. About 18 rursiradiate primary ribs terminate in prominent bullae on the umbilical shoulder of the final whorl, from which fasciculate bundles of commonly three, rarely only two, secondary ribs arise, generally with an intercalated rib between bundles. The coarse secondaries are prorsiradiate, recurving slightly so as to cross the venter transversely. There may be a slight inflexion of the secondaries as they cross the siphonal line. The umbilical wall is steep, with a subrounded umbilical shoulder. The whorl section is rather variable. Whilst parabolae are lacking on the phragmocone, the peristome is provided with a typical parabola, viz. a deep, oblique constriction bordered both adorally and adapically by prominent ribs, the adapical one of which is prominently flared. The adoral rib is provided with well-developed, slightly converging lateral lappets. There are between 8–10 secondaries per 3 bullae on the final whorl with between 7 and 9 secondaries within a 30 mm distance along the venter.

Macroconch (♀): shell large, with peristome preserved at 200 mm diameter; strongly inflated, cadicone, involute up to the umbilical bullae on the inner whorls, with about 80 per cent of the preceding whorl being covered, but becoming slightly evolute on the final whorl as the umbilical seam egresses, so as to make a short distance of secondary ribbing visible below the umbilical seam. Prominent primary ribs begin at, or close to, the umbilical seam and curve backwards (virguliform) to terminate in 17–25 prominent bullae on the umbilical shoulder. Each bulla gives rise to bundles of 3–5 prorsiradiate secondaries, generally with 1–2 intercalated ribs between bundles, so that there are between 10 and 17 secondaries per 3 bullae. The secondaries recurve slightly so as to cross the venter transversely. At diameters greater than 90 mm there are almost invariably 4 secondaries per bulla. At 75 mm diameter there are 10 ribs per 3 bullae, with a rib spacing across the venter of 3–4 mm. The whorl section is semicircular and rather depressed, with a broad, evenly-rounded venter. Parabolae are lacking at all growth stages. The peristome is seen to be preserved in a single specimen, BM–C47128, and is simple. The whorls of the macroconch show a steady rate of inflation. SAM–PCU1604 is preserved as an internal

Fig. 33. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♂). The specimen figured by Spath (1930) as *Rogersites* aff. *wilmanae* (Kitchin), BM–C32204, a probable microconch. × 1.

mould. It is moderately large and somewhat inflated, with a rather narrow umbilicus, and steep umbilical walls. Well-developed primaries terminate in small but distinct bullae on the umbilical shoulder, from which arise bundles of fine, prorsiradiate secondaries which very occasionally bifurcate at about mid-flank, with 1–2 intercalated ribs between bundles. There are 20 umbilical bullae on the outer whorl. Parabolae are lacking.

The following description of the holotype of *O. atherstoni* is based on a plastotype supplied by M. K. Howarth: the specimen is moderately large, and somewhat inflated, and appears to have much of the shell material preserved. The umbilicus is narrow and deep, with convex umbilical walls and a subrounded umbilical shoulder. Primary ribs begin at, or close to, the umbilical seam and pass strongly backwards (rursiradiate) to the umbilical shoulder where they terminate in small but prominent umbilical bullae, of which there are about 20 on the outer whorl. There are fewer umbilical bullae on the earlier whorls. From the umbilical bullae arise bundles of usually 4 fine secondary ribs, rarely 3 or 5, with commonly 2 intercalated ribs between bundles, although there may occasionally be one only. Thus, on the adoral portion of the outer whorl there are 37 secondaries per 7 bullae, with 26 ribs within a 100 mm distance along the venter. The outer whorl is not complete, but there were probably in all about 100 secondaries. Portion of an earlier whorl, evident in the broken umbilicus, shows ribbing to have been coarser at earlier growth stages, with secondaries generally arising in bundles of 3, with an intercalated rib between bundles. The whorl section is semicircular and depressed, with an evenly rounded venter. The whorls show a constant rate of inflation. Although the specimen is entirely septate, matrix on the outer whorl shows that the umbilical

seam of the following whorl egressed markedly, and that it represented the body whorl. There is no evidence for parabolae at any growth stage.

Specimen AM–4293 represents a typical juvenile. In this example, there are 17 bullae on the outer whorl, from which arise bundles of 2–3 prorsiradiate secondaries with an intercalated rib between bundles. There are 10 ribs per 3 bullae, with 13 secondaries within a 20 mm distance along the venter.

Measurements

No.	D	H	Wi	W/H	Uo	Ui
BM–C47128	197	81	*c.* 95	1,17	95	61 (31)
,,	*c.* 130	56	?	?	52	34 (26) (♀)
SAM–PCU1590	102	49	75	1,53	45	25 (25)
,,	80	34	52	1,53	29	16 (20) (♀)
SAM–PCU1604	98	48	67	1,40	35	*c.* 21 (21) (♀)
PEM–1468/74	72	33	36	1,09	30	21 (29) (♂)
SAM–PCU1529	58	*c.* 22	?	?	28	? ? (♂)
SAM–PCU1598	66	28	?	?	32	19 (29) (♂)
SAM–PCU1526	72	31	41	1,32	30	17 (24) (♂)
SAM–9242†	94	36	47	1,31	42	26 (28) (♂)
BM–C32202*	134	61	80	1,31	48	27 (20) (♀)
,,	106	51	66	1,29	36	23 (22)
,,	*c.* 80	40	53	1,32	28	17 (21)
BM–C32204‡	44	19	24	1,26	17	10 (23) (♂)

† The holotype of *Rogersites otoitoides* Spath.
* Plastotype of *O. atherstoni* (Sharpe).
‡ Specimen figured by Spath (1930) as *Rogersites* aff. *wilmanae* Kitchin.

Discussion

It is hardly necessary to point out the confusion that has surrounded Sharpe's species since its inception in 1856. This has been due to a number of factors. First and foremost is the marked homoeomorphy between *O. atherstoni* (♀) and macroconchs of other species. This, together with the comparison of different growth stages, the failure to recognize sexual dimorphism, and the placing of constricted forms within this species have all added to the confusion. Thus, this name has been used for species from the Crimea (Karakasch 1902), England (Pavlow *in* Pavlow & Lamplugh 1892), Mexico (Burckhardt 1906; Böse 1923), the Swiss Jura (Baumberger 1907), Pakistan (Spath 1939), South Africa (Kitchin 1908; Spath 1930), France (Collignon 1962), and Argentina (Riccardi *et al.* 1971).

Riccardi *et al.* (1971), in describing forms of *Olcostephanus* from the Lower. Cretaceous of west-central Argentina, assigned their entire olcostephanid fauna '. . . to the almost cosmopolitan *Olcostephanus atherstoni* (Sharpe)'. They place into synonymy with Sharpe's holotype, which they take to represent a macroconch, the following species: *O. schenki* (Oppel), *O. sudandina* (Windhausen),

Fig. 34. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♂). The holotype of *Rogersites tenuicostatus* Imlay from the Taraises Formation of northern Mexico (after Imlay 1937). × 1.

and with reservation *O. curacoensis* (Weaver) and *O. sublaevis* Spath. The microconch is taken to be represented by the synonymous species *O. psilostomus* Neumayr & Uhlig, *O. wilmanae* (Kitchin), and *O. midas* (Leanza). Moreover, these authors hint that *O. otoitoides* (Spath), *O. wynnei* Spath, *O. baini* (Sharpe), *O. baini* var. *ambikyi* (Besairie), *O. auritus* (Leanza), *O. salinarius* Spath, *O. sphaeroidalis* (Spath), *O. glaucus* Spath, *O. rigidus* (Baumberger), *O. leptoplanus* (Baumberger), *O. imbricatus* (Baumberger), and *O. modderensis* (Kitchin) were a group of doubtfully distinct species over which *O. atherstoni* had priority.

These authors have, however, been misled both by the convergence between macroconch forms, and in neglecting the specific importance of parabolic constrictions.

The microconch is represented, amongst South African material, by *O. otoitoides* (Spath) (Fig. 30), the crushed *O. wilmanae* (Kitchin) (Fig. 32) and the specimen figured by Spath (1930) as *Rogersites* aff. *wilmanae* (Fig. 33). Other synonyms certainly include *O. tenuicostatus* (Imlay) (Fig. 34), *O. prorsiradiatus* (Imlay) (Fig. 35), and *O. neoleonensis* (Cantu Chapa) (Fig. 36), the latter species based upon the inner whorls of *O. prorsiradiatus*, as well as *O. psilostomus* (Pictet) (Fig. 37), *O. midas* (Leanza) (Fig. 38), *O. leptoplanus* (Baumberger) (Fig. 39), of which *Astieria psilostoma* var. *picteti* Wegner (1909) is a junior objective synonym, and possibly *O. curacoensis* (Weaver) (Fig. 40).

Astieria sudandina Windhausen (1931) (Fig. 41) was based upon a specimen illustrated only in lateral view, without scale, description or locality, and is thus a *nomen nudum*. According to Riccardi *et al.* (1971), it is a synonym of *O. atherstoni*.

Maderia altiumbilicata Imlay (1938) was based upon a strongly inflated, globose, pyritic nucleus with a strongly depressed, semilunate whorl section.

Fig. 35. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♀). The holotype of *Rogersites prorsiradiatus* Imlay from the Upper Valanginian of the Taraises Formation of northern Mexico (after Imlay 1937). × 1.

Fig. 36. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe). The holotype of *Taraisites neoleonense* Cantu Chapa from the Taraises Formation of northern Mexico (after Imlay 1937). × 1.

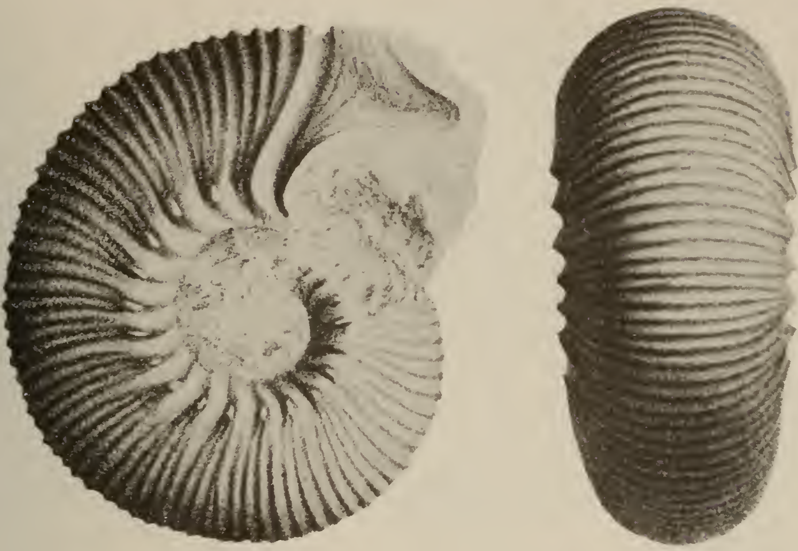

Fig. 37. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♂). The holotype of *Olcostephanus psilostomus* Neumayr & Uhlig from northern Germany (after Neumayr & Uhlig 1881). × 1.

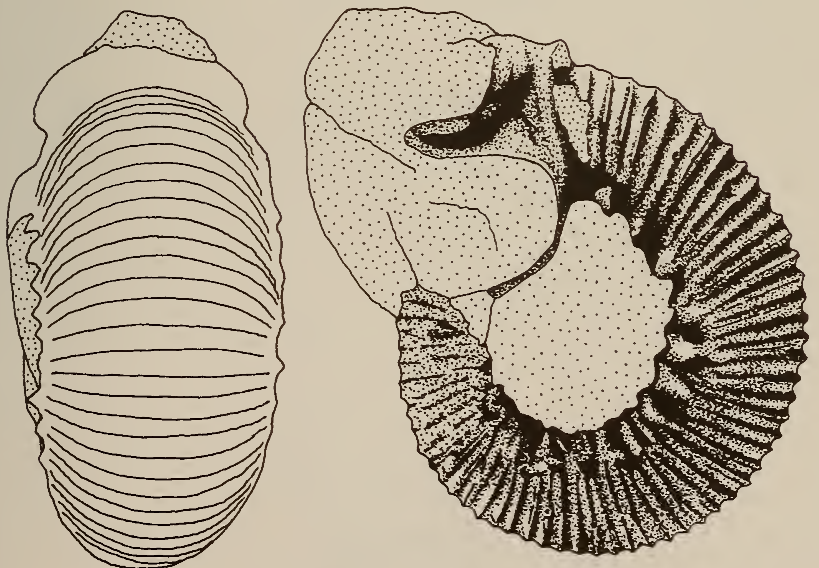

Fig. 38. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♂). The holotype of *Holcostephanus midas* Leanza from the Upper Valanginian of Neuquén, Argentina (after Leanza 1944). × 1.

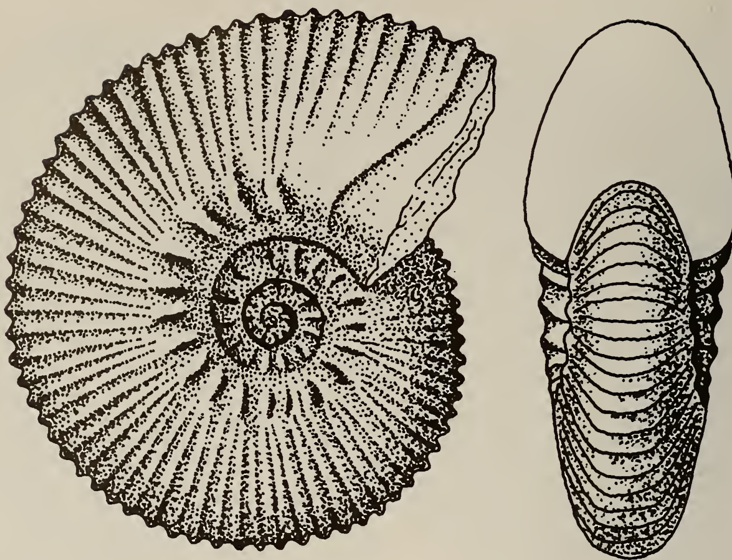

Fig. 39. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♂). The original of this specimen is the type of *Holcostephanus leptoplanus* Baumberger, by lectotype designation herein, and also of *Holcostephanus* (*Astieria*) *psilostomus* var. *picteti* Wegner (after Pictet & Campiche 1858). × 1.

Ornament comprises 16–17 primary ribs which terminate in bullae on the umbilical shoulder from which arise bundles of three prorsiradiate secondaries. Parabolae are lacking, and the writer believes this species to be based upon a nucleus of *O. atherstoni.*

As can be seen from Figures 42–43, *Rogersites curvicostatus* Besairie (1936) is merely based upon a macroconch of *O. atherstoni* whilst, according to Thieuloy (1977*b*: 126), *Astieria carpathica* Jekelius (1913) is also a synonym of Sharpe's species.

Taraisites bosei Cantu Chapa (Fig. 9) was erected for the poorly preserved specimen figured by Böse (1923: 76, pl. 2, figs 3–5) as *Astieria* aff. *baini*, and made the type of the genus *Taraisites.* This fragment appears to be specifically indeterminate; it may be either *O. baini* or a juvenile *O. atherstoni.* It is best regarded as a *nomen dubium*, not to be used.

Olcostephanus actinotus (Baumberger) (Fig. 44) is a rather large species, probably an immature macroconch, with a deep umbilicus and steep walls ornamented with 17–18 slender, rursiradiate primaries terminating in bullae. From these commonly arise 4, occasionally 3 or 5, secondaries with 1–2 intercalated ribs between bundles. Parabolae are lacking. This species seems to differ from *O. atherstoni* in its more compressed form with a subtrigonal whorl section, and in its straight not sinuous secondary ribs.

Olcostephanus andartae Thieuloy (1972) (Fig. 45) has a depressed whorl section with steep umbilical walls. On the outer whorl, 14–15 primary ribs

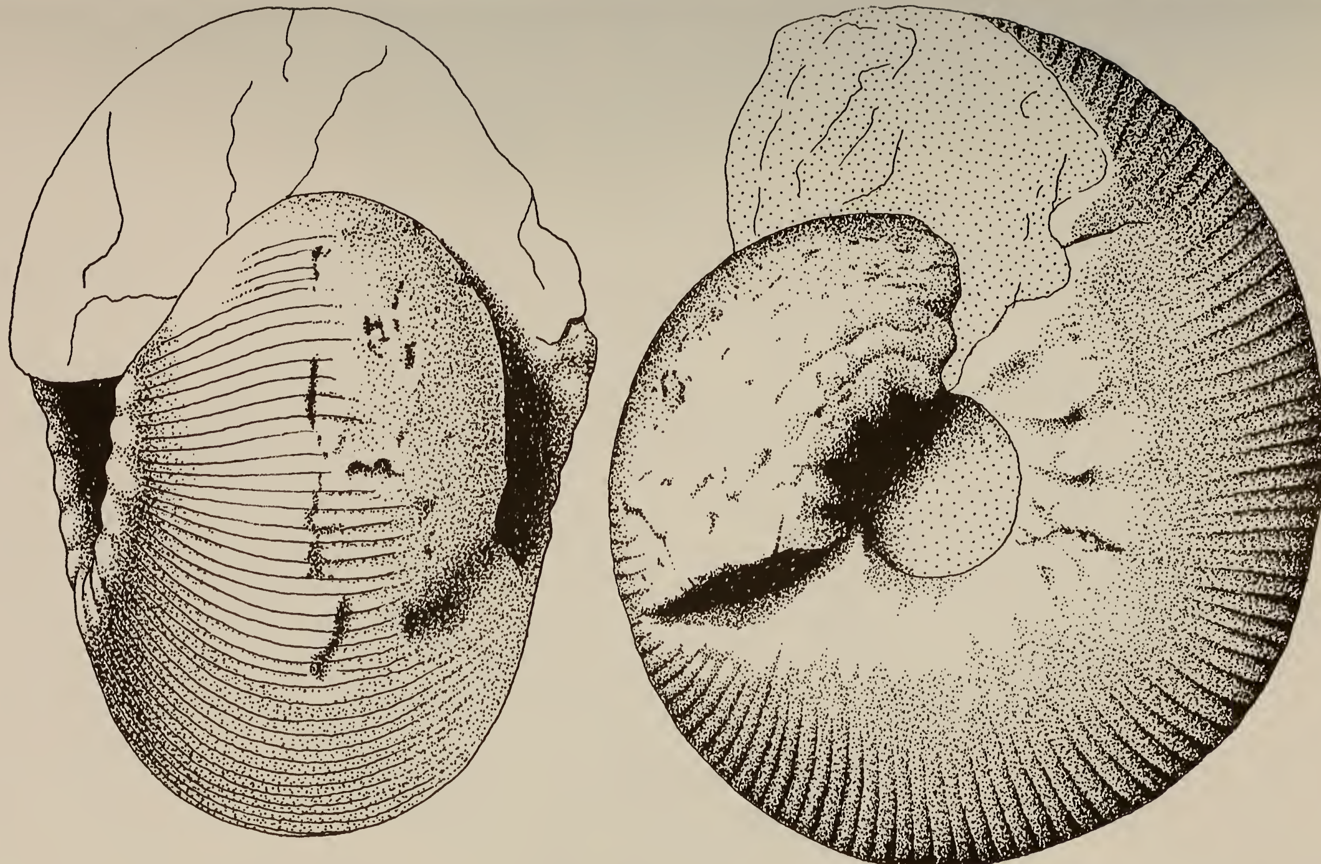

Fig. 40. *Olcostephanus* (*Olcostephanus*) cf. *atherstoni* (Sharpe) (♀). The holotype of *Astieria curacoensis* Weaver from Neuquén, Argentina (after Weaver 1931). × 1.

Fig. 41. *Olcostephanus* (*Olcostephanus*) cf. *atherstoni* (Sharpe) (♀). The holotype, by monotypy, of *Astieria sudandina* Windhausen, a *nomen nudem* since it was not described, whilst the scale and locality are also unknown (after Windhausen 1931). × 1.

terminate in prominent rounded tubercles on the umbilical shoulder and give rise to bundles of 3–4 coarse, prorsiradiate secondaries characterized by frequent bifurcation at midflank. Parabolae are lacking. This species differs from *O. atherstoni* in its coarser, more distant ribbing with frequent bifurcation and in possessing swollen, rounded umbilical tubercles. *Olcostephanus bossingaulti* (d'Orbigny) (Fig. 46), of which *O. laticosta* (Gerth) (Fig. 47) is merely based upon a juvenile, is an Hauterivian species which is very close to *O. andartae*, but seems to lack bifurcating secondaries.

'*Simbirskites*' *araucanus* Leanza (1957) is a moderately large, fairly evolute species of *Olcostephanus*, with inclined umbilical walls ornamented with about 20–23 prorsiradiate primaries per whorl. These terminate in prominent umbilical bullae which generally give rise to three radial, to slightly prorsiradiate secondaries, frequently with an intercalated rib between bundles. There are about seventy secondary ribs per whorl, a short distance of which are exposed in the umbilicus, beneath the umbilical seam. Parabolae lacking. This species differs from the microconch of *O. atherstoni* in its more evolute form, with sloping umbilical walls and prorsiradiate primaries, and should be assigned to the subgenus *Subastieria*. It seems likely that the Sardinian *O.* (*Subastieria*) *nicklesi* Wiedmann & Dieni (Fig. 48) is merely based upon juveniles of this species.

Fig. 42. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♀). Lateral view of the holotype of *Rogersites curvicostatus* Besairie, in the collections of the University of Paris. × 1.

Fig. 43. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♀). Front view of the holotype of *Rogersites curvicostatus* Besairie, in the collections of the University of Paris. × 1.

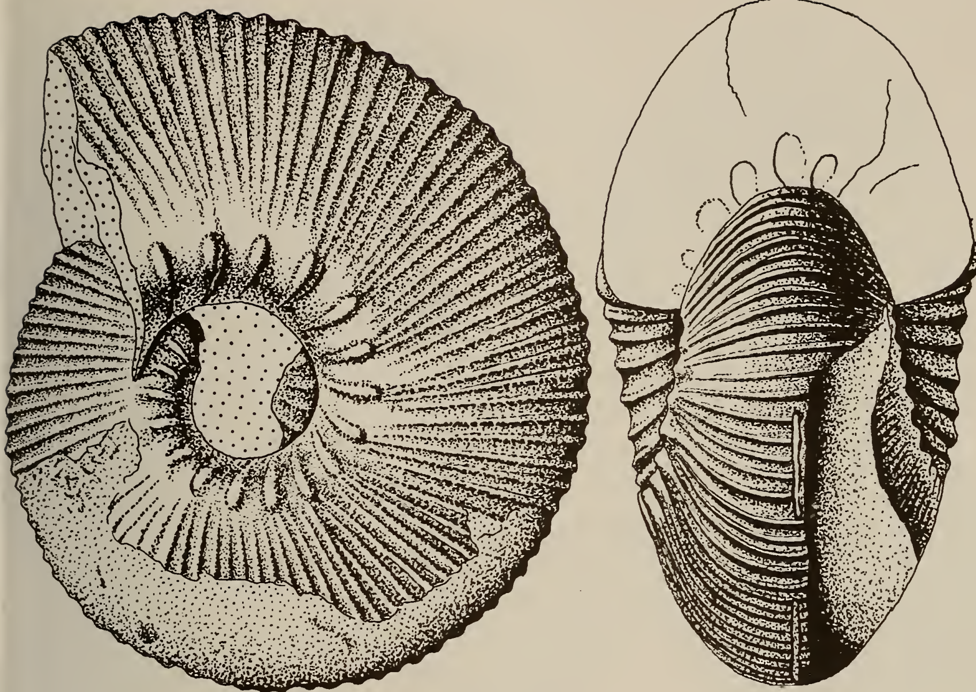

Fig. 44. *Olcostephanus* (*Olcostephanus*) *actinotus* (Baumberger) (♀), from the Swiss Jura (after Baumberger, 1908). × 1.

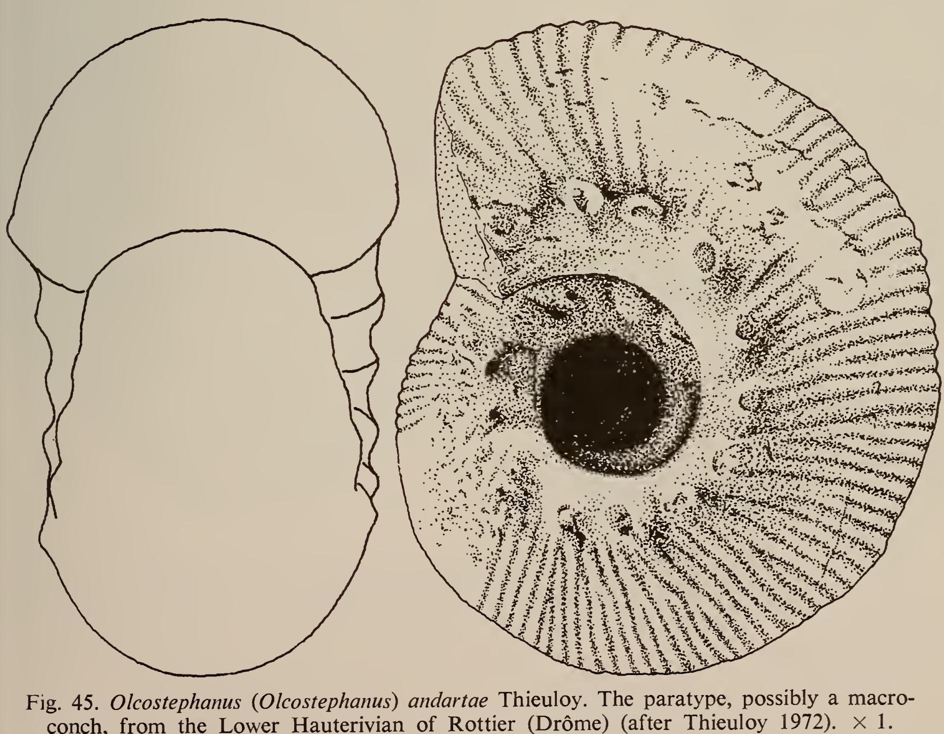

Fig. 45. *Olcostephanus* (*Olcostephanus*) *andartae* Thieuloy. The paratype, possibly a macroconch, from the Lower Hauterivian of Rottier (Drôme) (after Thieuloy 1972). × 1.

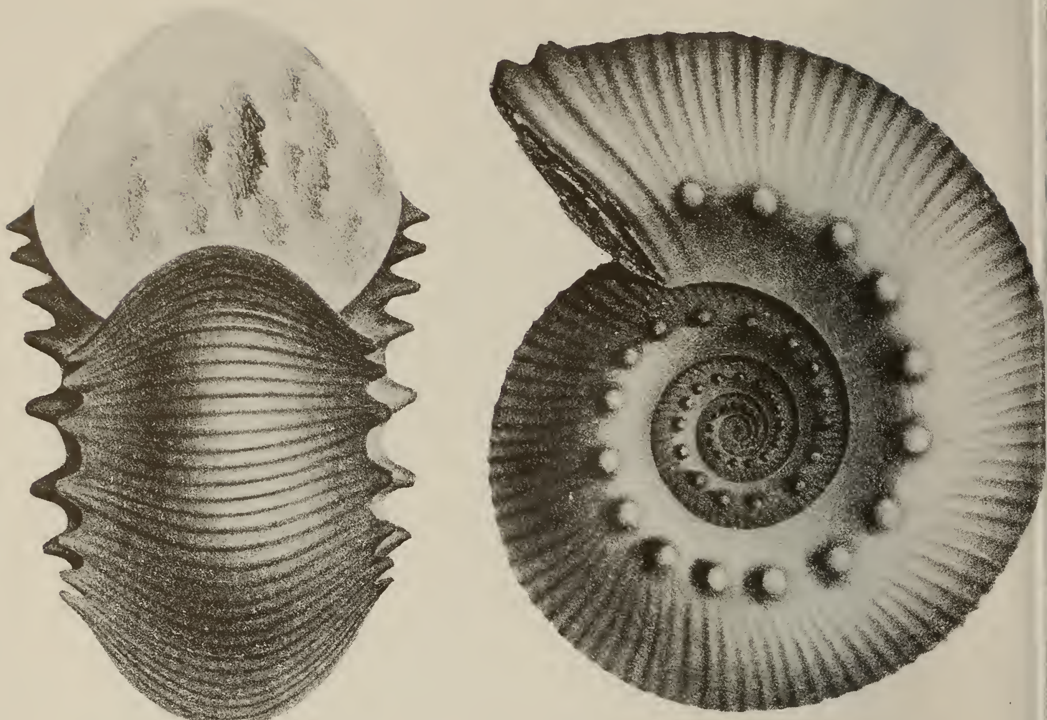

Fig. 46. *Olcostephanus* (*Olcostephanus*) *bossingaulti* (d'Orbigny) (♀). The holotype, by monotypy, from Colombia (after d'Orbigny 1842*b*). × 1.

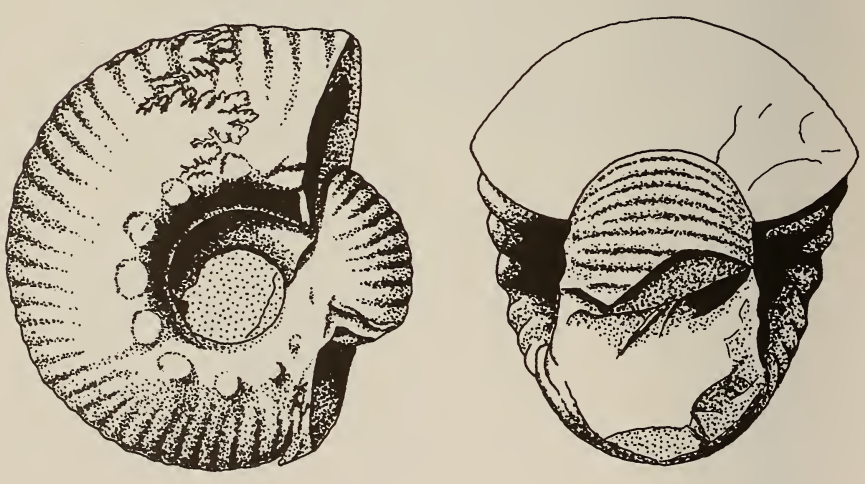

Fig. 47. *Olcostephanus* (*Olcostephanus*) *bossingaulti* (d'Orbigny). The holotype of *Astieria laticosta* Gerth from Neuquén, Argentina (after Gerth 1925). × 1.

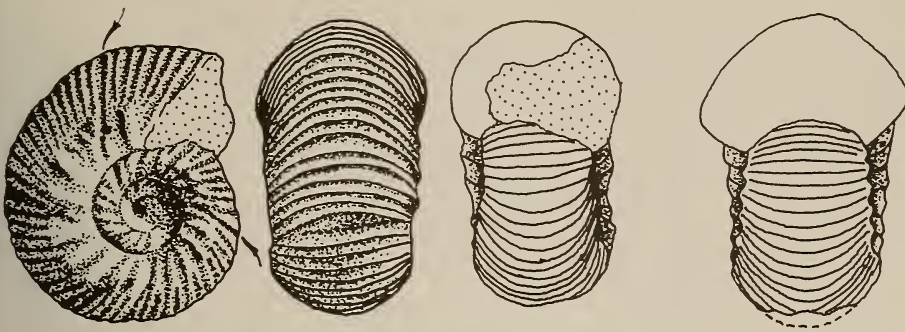

Fig. 48. *Olcostephanus* (*Subastieria*) *nicklesi* Wiedmann & Dieni. The holotype and front view of a paratype from the Upper Valanginian of Sardinia (after Wiedmann & Dieni 1968). × 1.

Fig. 49. *Olcostephanus* (*Olcostephanus*) *bernardensis* (Lory) (♀). A cast of the holotype MNHP–R3111, from the Middle Hauterivian of the Hautes-Alpes. × 1.

A cast of the holotype of *Olcostephanus bernardensis* (Lory) (Fig. 49)* in the Natural History Museum, Paris, with the number MNHP–R3111, shows this species to be moderately involute (umbilicus 28% of the diameter), with a strongly compressed whorl section (W/H = 0,75). On the outer whorl, nineteen rursiradiate primaries terminate in bullae which give rise to bundles of prorsiradiate secondary ribs. The secondaries sometimes bifurcate on the flanks so that there are about 115 ribs across the venter of the final whorl. Parabolae are lacking and the peristome appears to be simple. This species seems to differ from the *O. atherstoni* macroconch in being somewhat more densely ribbed, with more frequent bifurcation of secondaries.

'*Maderia*' *cupidinensis* Imlay (1938) was based upon a pyritic nucleus with a strongly depressed, semilunate whorl section. Between 20 and 22 primary ribs terminate in umbilical bullae from which arise 2–3 slightly prorsiradiate secondaries. Parabolae are lacking. This species seems to differ from *O. atherstoni* in the shape of the whorl section, and in being less inflated. It closely approaches *O. andartae* Thieuloy.

Fig. 50. *Olcostephanus* (*Olcostephanus*) *crassus* (Zwierzycki) (♀). The holotype, by monotypy, from the Tendaguru Formation of Tanzania (after Zwierzycki 1914). × 1.

Olcostephanus crassus (Zwierzycki) (Fig. 50) is based upon a poorly preserved macroconch which approaches *O. atherstoni*, but should be regarded as specifically indeterminate, a *nomen dubium*.

Olcostephanus discoideus Imlay (Fig. 51) is a probable macroconch with a compressed ovate whorl section, the compression seemingly enhanced by crushing. About 20 primaries terminate in small bullae on the umbilical shoulder from which arise 3, rarely 2 or 4, radial secondaries with 1–2 intercalated ribs

* This figure and various others are not up to our usual standard; some are from published illustrations and others cannot be replaced—Ione Rudner, Editor.

Fig. 51 *Olcostephanus* (*Olcostephanus*) *discoideus* Imlay (♀). The holotype from the Taraises Formation of northern Mexico. (after Imlay 1938). × 1.

between bundles. On the adoral three-quarters of the outer whorl, the adapical rib of most bundles bifurcates. Its strongly compressed form separates Imlay's (1938) species from *O. atherstoni.*

Olcostephanus irregularis (Wegner) (Fig. 52) is a strongly compressed (?crushed), moderately evolute form with steep umbilical walls. About fifteen umbilical bullae per half whorl give rise to bundles of commonly three, slightly prorsiradiate secondaries which frequently bifurcate near midflank. There are occasional intercalatories between bundles. Parabolae lacking. This species differs from *O. atherstoni* in its more compressed form, more numerous umbilical bullae and frequent bifurcation of secondaries.

A cast of *Olcostephanus lamberti* (Kilian) (Fig. 53), MNHP–R3110, shows the original to have been somewhat eroded and slightly distorted. The whorl section is distinctly compressed, elliptical, and the umbilicus fairly wide with convex, rather sloping, umbilical walls. There are thirteen slightly rursiradiate, almost radial, primary ribs per whorl which terminate in rather prominent bullae at the umbilical shoulder. From these arise bundles of 3–4 rather coarse, prorsiradiate secondaries with intercalated ribs between bundles. The secondary ribs are about as wide as the interspaces and there are 65–70 on the outer whorl.

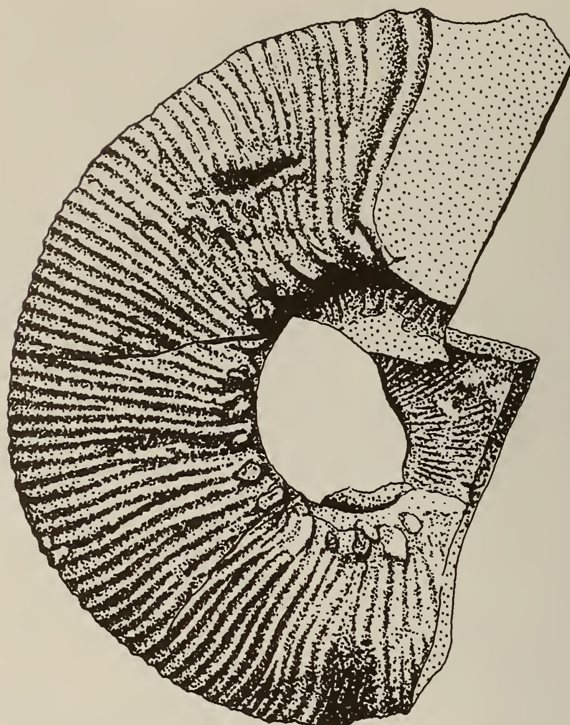

Fig. 52. *Olcostephanus* (*Olcostephanus*) *irregularis* (Wegner) (♀). The holotype, by monotypy, from the Lower Hauterivian of Marignac (Drôme) (after Wegner 1909). × 1.

Parabolae are lacking but there is a prominent apertural constriction. This species resembles *O. atherstoni* but may be distinguished by its more compressed form, fewer umbilical bullae and its younger (mid-Hauterivian) age.

Olcostephanus fascigerus Spath (Figs 92–97) differs from *O. atherstoni* in its finer, thread-like secondary ribs with more intercalatories between bundles, its more prominent bullae, and its constant rate of inflation which gives Spath's (1939) species a cylindrical aspect in ventral view.

The microconch of *O. baini baini* (Sharpe) (Fig. 114) differs from that of *O. atherstoni* in being smaller with somewhat fewer secondary ribs per whorl, and in possessing parabolae. The *O. baini* var. *sphaeroidalis* (Spath) microconch (Figs 145–146, 149) differs from *O. atherstoni* (♂) in possessing parabolae.

Within the Uitenhage fauna, *O. atherstoni* macroconchs are rather rare and only five further specimens, one of which is fragmentary, are without hesitation assigned to Sharpe's species. However, very common are large macroconchs which differ from the holotype of *O. atherstoni* in the greater inflation of their middle whorls and their more depressed whorl section (Fig. 118). Whilst the differences may appear slight, the holotype of *O. baini*

Fig. 53. *Olcostephanus* (*Olcostephanus*) *lamberti* (Kilian). A cast of the holotype, MNHP–R3110, from the Middle Hauterivian of Montbrand, Hautes-Alpes. × 1.

var. *sphaeroidalis* (Spath) shows that in addition the inner whorls of these more inflated forms bear parabolae. As such, the similarities merely provide further evidence of the perturbing homoeomorphy between adult macroconchs of *Olcostephanus*.

Occurrence

Olcostephanus atherstoni is a widely distributed species which is at present recorded from South Africa, Madagascar, Argentina, northern Mexico, Morocco, France, Austria, Switzerland and Germany but, rather curiously, not yet from Pakistan.

Olcostephanus (*Olcostephanus*) *densicostatus* (Wegner, 1909)

Figs 27E–F, 54–55

Microconch (♂)

? *Olcostephanus salinarius* Spath, 1939: 13, pl. 1 (figs 1–3, 6–7 only), pl. 2 (fig. 5), pl. 19 (fig. 4), pl. 20 (fig. 2). Fatmi, 1977: 266, pl. 1 (figs 5–6), pl. 2 (fig. 4), pl. 3 (fig. 1).
? *Holcostephanus auritus* Leanza, 1944: 18, pl. 2 (fig. 1).
? *Holcostephanus busnardoi* Collignon, 1962: 43, pl. 191 (fig. 868).

Macroconch (♀)

Non Holcostephanus atherstoni Sharpe var. nov., Kilian, 1902: 865, pl. 57 (fig. 1) (= ? *O. ventricosus* (von Koenen)).
Holcostephanus (*Astieria*) *atherstoni* var. *densicostata* Wegner, 1909: 82, pl. 16 (fig. 3).
? *Astieria multistriata* Zwierzycki, 1914: 53, pl. 6 (figs 6–9, 16).
? *Rogersites sakalavensis* Besairie, 1936: 139, pl. 13 (figs 10–12).
? *Rogersites spathi* Besairie, 1936: 140, pl. 12 (figs 1–2).
? *Rogersites filifer* Imlay, 1937: 559, pl. 73 (figs 1–2), pl. 74 (figs 4–5).
Olcostephanus densicostatus (Wegner) Spath, 1939: 27.
Rogersites atherstoni var. *densicostatus* (Wegner) Tzankov, 1943: 197, pl. 9 (figs 1–3).

Material

A single juvenile, SAM–PCU1612, without locality data but presumably from the Sundays River Formation.

Holotype

By lectotype designation herein, the original of the specimen of *Holcostephanus* (*Astieria*) *atherstoni* var. *densicostata* figured by Wegner (1909: 82, pl. 16 (fig. 3)) (Fig. 54) from Escragnolles (Alpes Maritimes).

Diagnosis

A species resembling *O. atherstoni* (Sharpe) but with finer, more numerous secondaries (Fig. 55). In the presumed microconch there are between 54 and 75 secondaries per half whorl, with well in excess of 60 per half whorl in the macroconch.

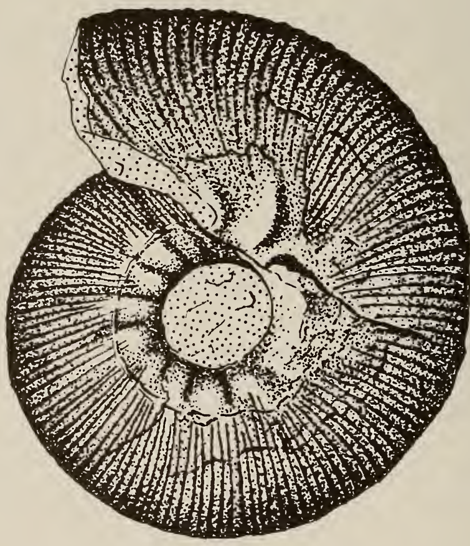

Fig. 54. *Olcostephanus* (*Olcostephanus*) *densicostatus* (Wegner). The holotype, by lectotype designation herein, from the Lower Hauterivian of Escragnolles (after Wegner 1909). × 1.

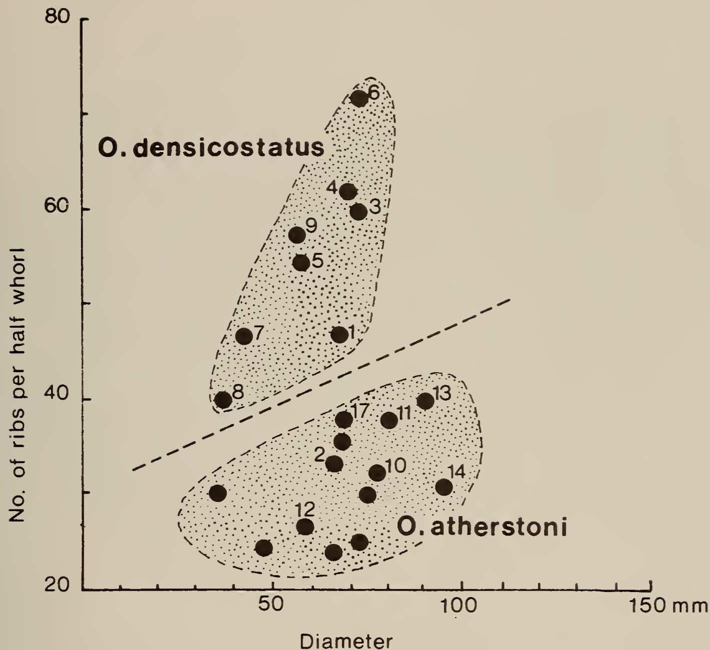

Fig. 55. Plot of rib density versus diameter for microconchs of *O. atherstoni* and the *O. densicostatus* plexus. 1 = *O. salinarius* var. *crassa* Spath, 2 = *O. midas* (Leanza), 3 = *O. densicostatus* (a probable macroconch), 4 = *O. salinarius* Spath (the holotype), 5 = *O. salinarius* var. *involuta* Spath, 6 = *O. salinarius* var. *obesa* Spath, 7 = *O. salinarius* sp. juv. (in Spath 1939), 8 = *O. salinarius* sp. juv. (in Spath 1939), 9 = *O. auritus* (Leanza), 10 = *O. atherstoni* (♂) (in Riccardi *et al.* 1971), 11 = *O.* aff. *wilmanae* (in Spath 1930), 12 = SAM–PCU1526, 13 = *O. wilmanae* (Kitchin), 14 = *O. otoitoides* (Spath), 15 = *O. tenuicostatus* (Imlay), 16 = *O. prorsiradiatus* sp. juv. (in Imlay 1937), 17 = *O. leptoplanus* (in Pictet & Campiche 1860).

Description

A single juvenile (Fig. 27E–F), preserved as a ferruginous internal mould, is referred, with reservations, to this species. The umbilicus is rather narrow and ornamented with about 18 bullae on the outer whorl. There are about 70 fine secondary ribs on the outer whorl (at a comparable diameter a juvenile *O. atherstoni* has only 60) but their connections with the umbilical bullae are indistinct. The whorl section is semicircular.

Discussion

The widespread occurrence of forms closely resembling *O. atherstoni* (Sharpe) but differing in the possession of denser secondary ribbing would seem to justify Spath's (1939: 27) elevation of Wegner's (1909) variety to specific rank. In his original description, Wegner also included the juvenile figured by Kilian (1902, pl. 57 (fig. 1)) into this species but Kilian's specimen shows a prominent parabola and is excluded from *O. densicostatus* as herein interpreted.

Fig. 56. *Olcostephanus* (*Olcostephanus*) *sakalavensis* (Besairie) (♀). The holotype in the collections of the University of Paris, from the Upper Valanginian of Ambiky, Madagascar. × 1.

Fig. 57. *Olcostephanus* (*Olcostephanus*) *sakalavensis* (Besairie). A hypotype in the collections of the University of Paris, from Ambiky, Madagascar. × 1.

Olcostephanus sakalavensis (Besairie) (Figs 56–57) is a strongly inflated macroconch species with a very depressed whorl section. The steep umbilical walls are ornamented with about 12 rursiradiate primaries per half whorl which terminate in bullae on the umbilical shoulder. From these arise bundles of 4–6, fine, prorsiradiate secondaries with intercalated ribs between bundles, so that there are 36 secondaries across the venter per 7 umbilical bullae on the outer whorl of the holotype. Parabolae are lacking at all growth stages. Modern revision of the European material will probably show that *O. sakalavensis* is a synonym of *O. densicostatus*.

Olcostephanus filifer (Imlay) (Fig. 58) was created for a large, strongly inflated macroconch with a broadly convex venter. The umbilicus of this species is narrow and deep, with vertical walls ornamented by 20 weak, rursiradiate primaries which terminate in rather weak tubercles at the umbilical shoulder. Each tubercle gives rise to 4–5 fine, prorsiradiate secondary ribs with 1–2 intercalated ribs between bundles. Parabolae are lacking. This species was said to differ from *O. densicostatus* in its finer ribbing and more numerous umbilical tubercles, but the differences are slight and probably do not warrant specific separation. *Olcostephanus filifer* is certainly a synonym of *O. sakalavensis*.

Olcostephanus spathi (Besairie) (Fig. 59) is based upon the inner whorls of a macroconch. It is a moderately inflated species with a semilunate, depressed whorl section. The umbilical walls are strongly convex and ornamented with 25 rursiradiate primaries which terminate in rather small umbilical bullae. From these arise bundles of slightly prorsiradiate, almost rectiradiate, secondaries whose connections with the umbilical bullae are indistinct. Between bundles there are several intercalated ribs, so that there are 33 secondaries across

Fig. 58. *Olcostephanus* (*Olcostephanus*) *filifer* (Imlay) (♀). The holotype from the Taraises Formation of northern Mexico (after Imlay 1937). × 1.

Fig. 59. *Olcostephanus* (*Olcostephanus*) *sakalavensis* (Besairie) (♀). The holotype of *Rogersites spathi* Besairie from the Upper Valanginian of Ambiky, Madagascar. × 1.

the venter per 8 umbilical bullae on the outer whorl of the holotype. Parabolae are lacking. This species is based upon the inner whorls of *O. sakalavensis* and is probably, therefore, a junior subjective synonym of *O. densicostatus.*

The holotype of *O. salinarius* Spath (Fig. 60) is a microconch, somewhat inflated and with a rather wide umbilicus. Rursiradiate primaries terminate in 20–24 umbilical bullae from which arise bundles of 4–5 fine, prorsiradiate secondaries. Parabolae are lacking. In view of the side-by-side occurrence of this species with *O. sakalavensis* in the Spiti Shales (Fatmi 1977) they are herein

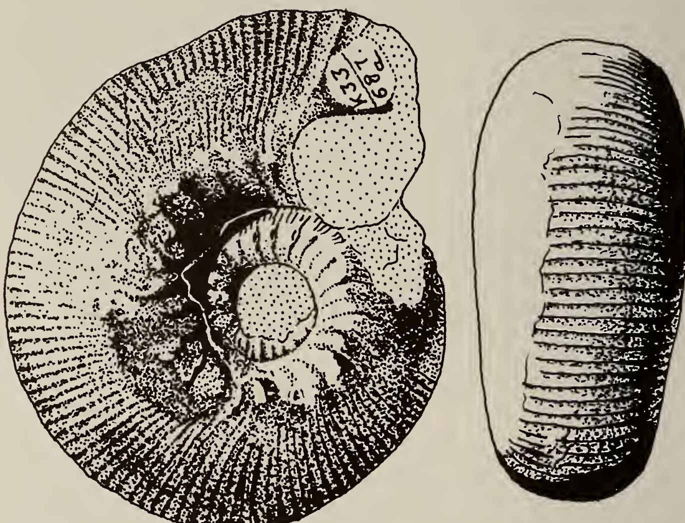

Fig. 60. *Olcostephanus* (*Olcostephanus*) *densicostatus* (Wegner) (♂). The holotype of *Olcostephanus salinarius* Spath from the Spiti Shales of Pakistan (after Spath 1939). × 1.

regarded as sexual dimorphs and *O. salinarius* is likely to become a junior subjective synonym of *O. densicostatus.* According to Fatmi (1977), *O. geei* Spath (Fig. 61) is a synonym of *O. sakalavensis.* As can be seen from Figure 62, *Holcostephanus auritus* Leanza is undoubtedly a synonym of *O. salinarius* and hence also probably based upon the microconch of *O. densicostatus.*

Olcostephanus bakeri (Imlay) (Fig. 63) is based upon an inflated macroconch with a semicircular whorl section and rursiradiate primary ribs which terminate in 11–12 small, pointed umbilical bullae per whorl. From these arise bundles of 4–5 secondaries which frequently bifurcate on the lower part of the flanks and with 1–2 intercalated ribs between bundles. Thus, there are about 120 ribs across the venter of the outer whorl. Parabolae are lacking. This species differs from *O. densicostatus* in possessing far fewer umbilical bullae and by showing more frequent bifurcation of the secondary ribs.

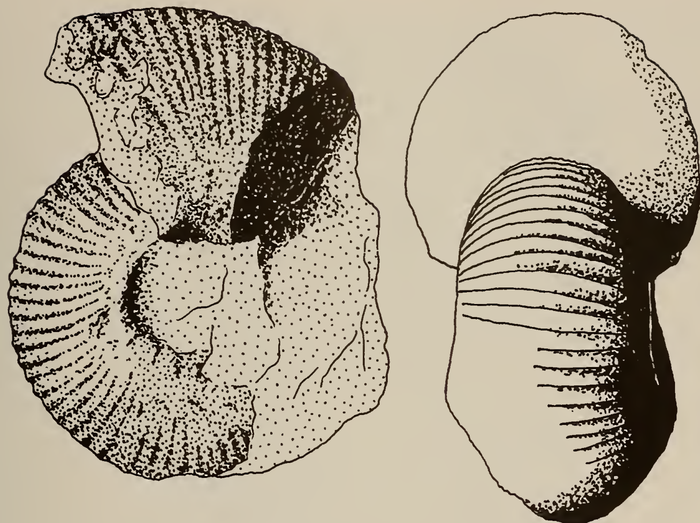

Fig. 61. *Olcostephanus* (*Olcostephanus*) *sakalavensis* (Besairie). The holotype of *Olcostephanus geei* Spath from the Spiti Shales of Pakistan (after Spath 1939). × 1.

Fig. 62. *Olcostephanus* (*Olcostephanus*) *densicostatus* (Wegner) (♂). The holotype of *Holcostephanus auritus* Leanza, from the Lower Hauterivian of Argentina (after Leanza 1944). × 1.

Fig. 63. *Olcostephanus* (*Olcostephanus*) *bakeri* (Imlay) (♀). The holotype from the Taraises Formation of northern Mexico (after Imlay 1937). × 1.

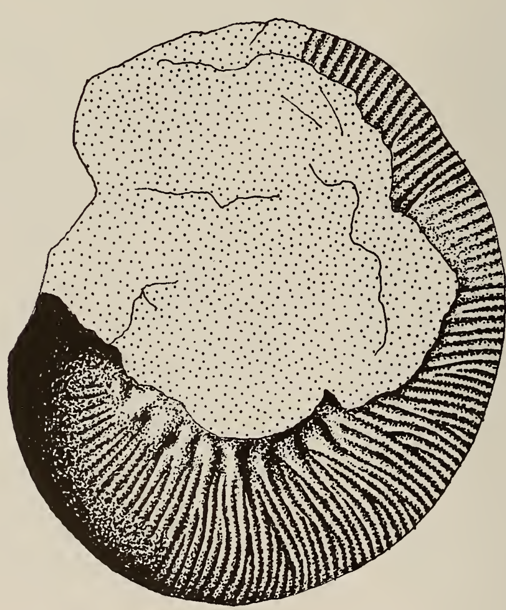

Fig. 64. *Spiticeras*? *balestrai* (Rodighiero). The holotype of *Astieria balestrai* Rodighiero, from Venice (after Rodighiero 1919). × 1.

'*Astieria*' *balestrai* Rodighiero (Fig. 64) resembles the presumed microconchs of *O. densicostatus* but frequent trifurcation of the secondary ribs suggests it is better referred to the genus *Spiticeras*.

Olcostephanus busnardoi (Collignon 1962) is based upon what appears to be a microconch showing a wide, deep umbilicus with vertical walls. Small rounded tubercles on the umbilical shoulder give rise to bundles of 3–5 slightly prorsiradiate ribs, with intercalatories between bundles. Parabolae are lacking. It is doubtful whether this species can be satisfactorily distinguished from the suspected microconchs of *O. densicostatus*.

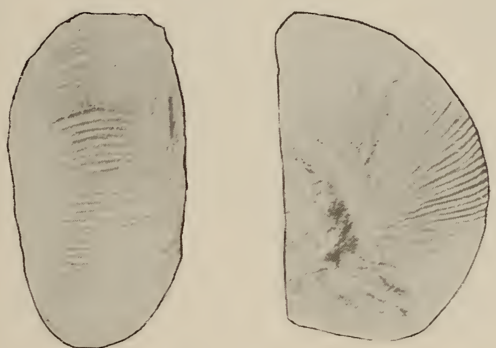

Fig. 65. *Olcostephanus delicatecostatus* Haas. The holotype from Colombia (after Haas 1960). × 1.

Olcostephanus delicatecostatus Haas (Fig. 65) from the Upper Valanginian of Colombia is characterized by '. . . the fineness and density of costation, there being nearly 25 ribs on a quarter whorl. . . . Some ribs bifurcate at about mid-flank. In one individual only 3 circumumbilical tubercles of medium strength are present. In the holotype . . . one or two narrow, extremely shallow constrictions are recognizable' (Haas 1960: 9). The density of ribbing in Haas's species is comparable to that of *O. densicostatus* but it can be distinguished by the irregular (?pathological) development of umbilical tubercles. What Haas (1960) refers to as constrictions in *O. delicatecostatus* do not seem to be parabolae but merely irregularities in growth.

Olcostephanus latiflexus (Baumberger 1908) (Fig. 66) is a moderately large, compressed form, with a wide rather shallow umbilicus and a very depressed whorl section. About 21 rursiradiate primaries on the outer whorl terminate in bullae from which arise 4–5 prorsiradiate secondaries with intercalated ribs between bundles. Parabolae appear to be lacking. This species is disturbingly close to *O. salinarius* and the other suspected microconchs of *O. densicostatus* and, as it has priority over Wegner's (1909) species, its affinities warrant closer scrutiny.

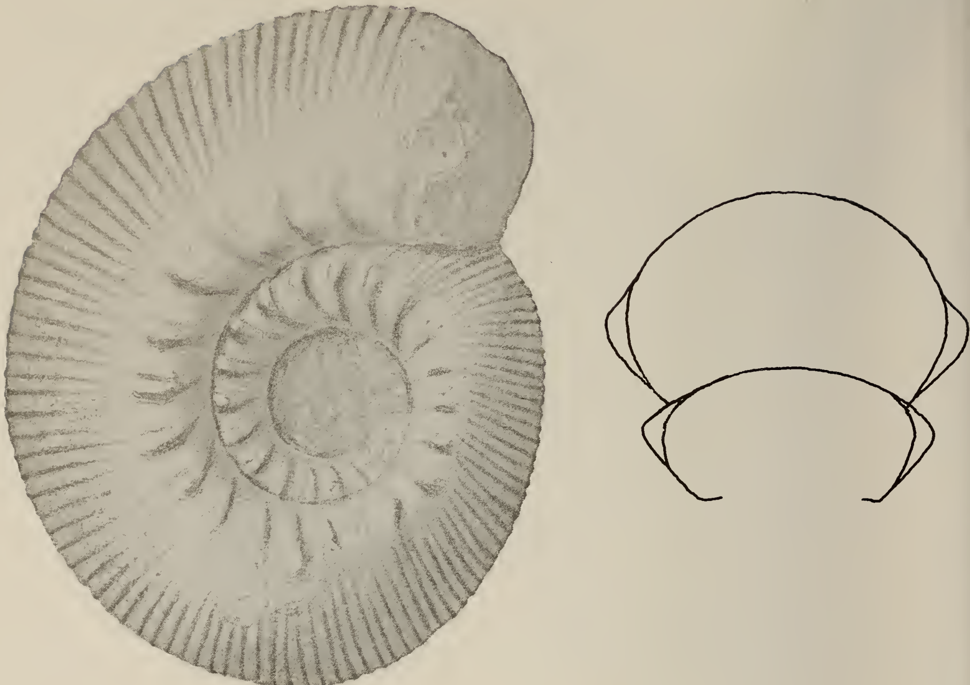

Fig. 66. *Olcostephanus* (*Olcostephanus*) *latiflexus* (Baumberger), (♂). The holotype, by lectotype designation herein, from the Swiss Jura (after Baumberger 1908). × 1.

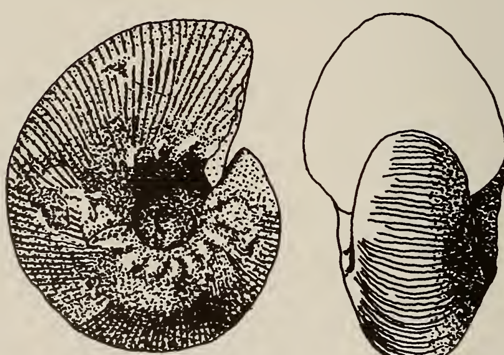

Fig. 67. *Olcostephanus* (*Olcostephanus*) *multistriatus* (Zwierzycki). The holotype, by lectotype designation herein, from the Lower Hauterivian of Tanzania (after Zwierzycki 1914). × 1.

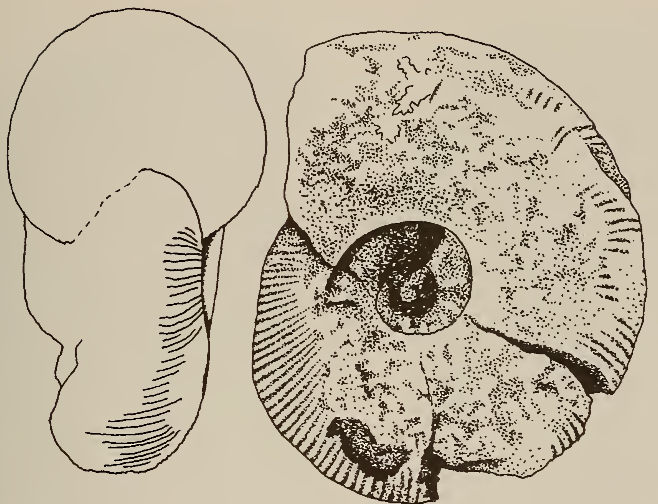

Fig. 68. *Olcostephanus* (*Olcostephanus*) *rebillyi* (Collignon). The holotype from the Lower Valanginian of Madagascar. (after Collignon 1962). × 1.

Olcostephanus multistriatus (Zwierzycki) (Fig. 67) is based upon a juvenile which does not seem to warrant specific separation from *O. densicostatus*.

Olcostephanus rebillyi (Collignon) (Fig. 68) is a species, allegedly from the Lower Valanginian, which is characterized by its rounded whorl section, relatively flat inner flanks, and by the fineness of its ornament which consists of extremely small tubercles from which arise bundles of very fine, prorsiradiate secondaries. Parabolae are apparently lacking. It was said to differ from *O. salinarius* in its narrower umbilicus, less inflated form and more flexuous ribs, but the differences are slight. In view of its age, however, Collignon's (1962) species is for the present maintained as distinct.

Olcostephanus rabei (Besairie) (Fig. 69) shows few features to distinguish it from *O. sakalavensis* and may also prove to a synonym of *O. densicostatus*.

Occurrence

Olcostephanus densicostatus is present in the Swiss Jura and perhaps Pakistan, Madagascar, Tanzania, South Africa, and Mexico.

Olcostephanus (*Olcostephanus*) *rogersi* (Kitchin, 1908)
Figs 70–73, 74A–B, 75A–B, 76, 80, 150E–G

Microconch (♂)

Holcostephanus rogersi Kitchin, 1908: 201, pl. 9 (fig. 1), pl. 10 (fig. 3). Hatch & Corstorphine, 1909: 303, fig. 76c. Giovine, 1950: 39.
Holcostephanus (*Astieria*) *rogersi* Kitchin, Wegner, 1909: 88.
Rogersites rogersi (Kitchen) Spath, 1930: 147. Besairie, 1936: 141.
Rogersites crassicostatus Spath, 1930: 199.
Olcostephanus (*Olcostephanus*) *madagascariensis* (Lemoine) Fatmi, 1977: 271, pl. 5 (fig. 4).

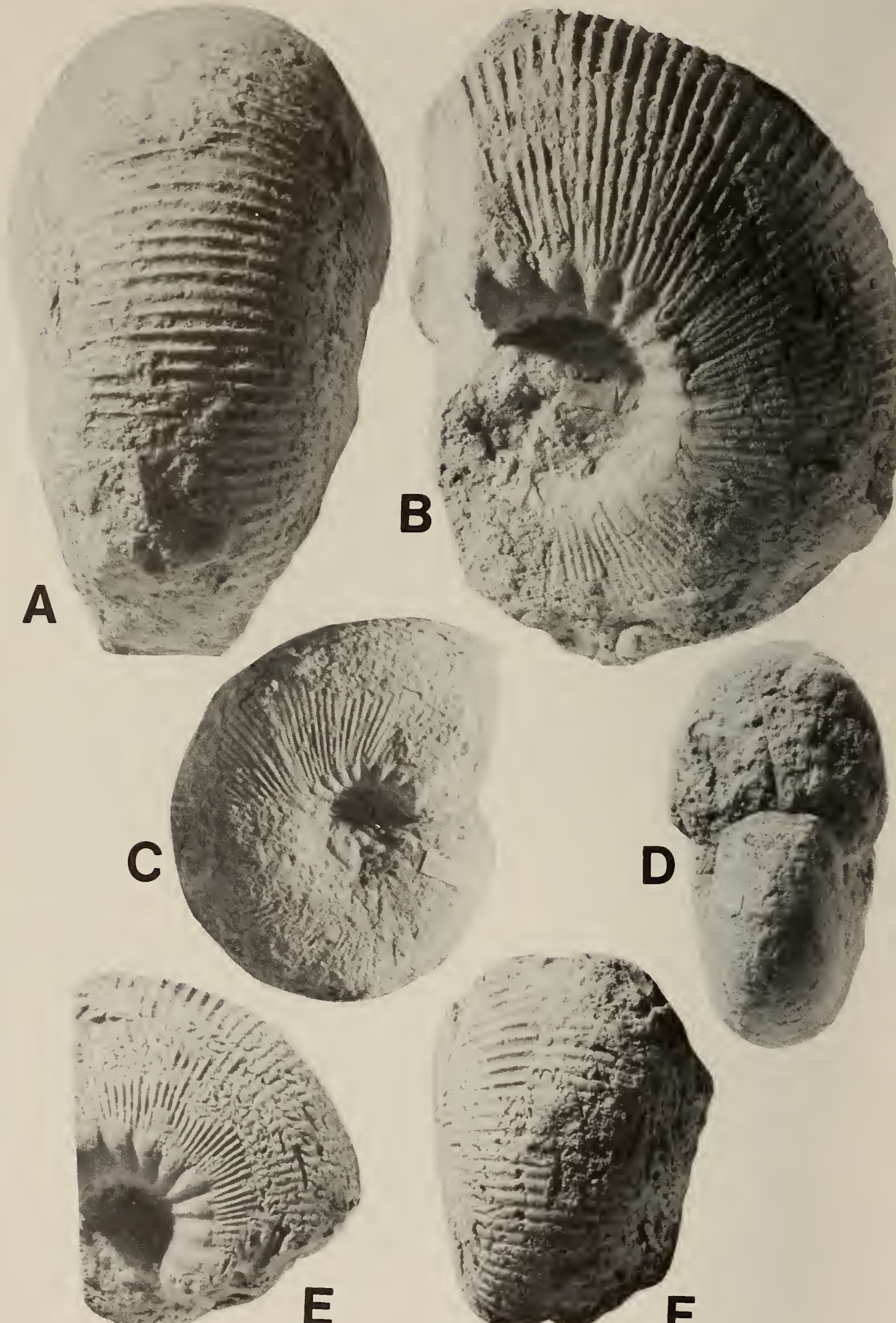

Fig. 69. *Olcostephanus* (*Olcostephanus*) *rabei* (Besairie), × 1. A–B. The holotype. C–F. Paratypes. From the Upper Valanginian of Madagascar.

Macroconch (♀)

Holcostephanus modderensis Kitchin, 1908: 202, pl. 10 (fig. 3). Giovine 1950: 39.
? *Astieria imbricata* Baumberger, 1908: 14, figs 123–125, pl. 26 (figs 2–3).
Holcostephanus (*Astieria*) *modderensis* Kitchin, Wegner, 1909: 89. Kilian 1910: 214.
Rogersites modderensis (Kitchin) Spath, 1924: 86. Spath, 1930: 148.
? *Holcostephanus* (*Rogersites*) *leanzai* Giovine, 1950: 38, pl. 2 (figs 1–3).
Rogersites kitchini Spath, 1930: 148, pl. 15 (fig. 4).
Olcostephanus modderensis (Kitchin) Riccardi *et al.*, 1971: 90.
Olcostephanus kitchini (Spath) Riccardi *et al.*, 1971: 90.

Material

14 specimens; 6 microconchs (SAM–4698, 5071, 11004, SAM–PCU1527, LJE–989b, PEM–1468/42), 7 macroconchs (SAM–PCU1542, 1566, LJE–989e, AAS–370, PEM–1465/81, BM–C47127, SAM–5070), and 1 juvenile (AM–4028).

Holotype

By monotypy, the original of *Holcostephanus rogersi*, SAM–5071 (Fig. 70D–G), figured by Kitchin (1908: 201, pl. 9 (fig. 2)) from the Sundays River Formation.

Diagnosis

Dimorphic. Microconch small (about 70 mm diameter), with 16 rursiradiate primaries per whorl, terminating in prominent umbilical bullae, from which arise invariably 3 coarse, radial secondaries, usually with an intercalated rib between bundles. Parabolae prominent. Macroconch large (300+ mm diameter), extremely inflated, globose. Inner whorls only with parabolae. About 18 very prominent umbilical tubercles on the outer whorls give rise to very coarse, radial secondaries, 3–4 per bulla, with 1–2 intercalated ribs between bundles.

Description

Microconch (♂): Kitchin's holotype, which is taken to represent a microconch, is a poorly preserved internal mould, with odd patches of recrystallized shell. Moreover, it has been slightly crushed, thereby leading Kitchin (1908) to believe the secondary ribbing to be rursiradiate. A near perfect example of this dimorph, LJE–989e, with the lappets preserved, shows, however, the true characters. In this latter specimen, the whorl section is rather depressed, with a fairly broad, evenly rounded venter, as in the holotype. The whorls are involute up to the umbilical bullae, except on the anterior portion of the body chamber when the umbilical seam egresses slightly to reveal a short distance of secondary ribbing of the penultimate whorl. The umbilicus is moderately wide and deep, with steep umbilical walls. The slope of the latter decreases slightly as the umbilical seam egresses.

The primary ribs begin at the umbilical seam and are prominently developed, curving backwards (rursiradiate) to sharp, prominent bullae on the umbilical shoulder. With the egression of the umbilical seam the primary

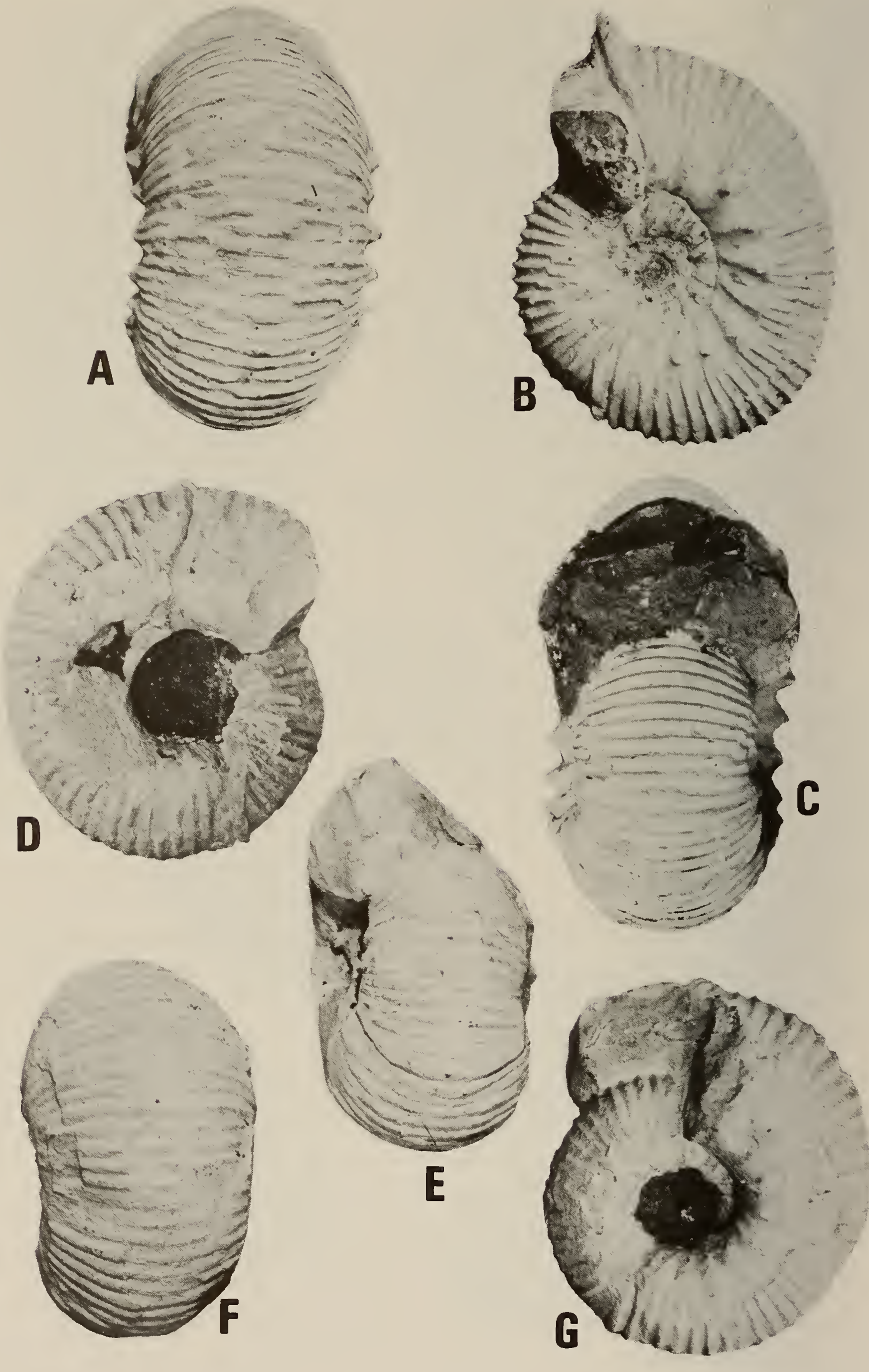

Fig. 70. *Olcostephanus* (*Olcostephanus*) *rogersi* (Kitchin) (♂), × 0,75. A–C. Ventral, lateral and front views of LJE–989*b*, with recrystallized test preserved, showing prominent umbilical bullae, radial secondaries, parabolae and lappets. D–G. Right lateral, front, ventral and left lateral views of the holotype, by monotypy, SAM–5071, based upon a poorly preserved internal mould.

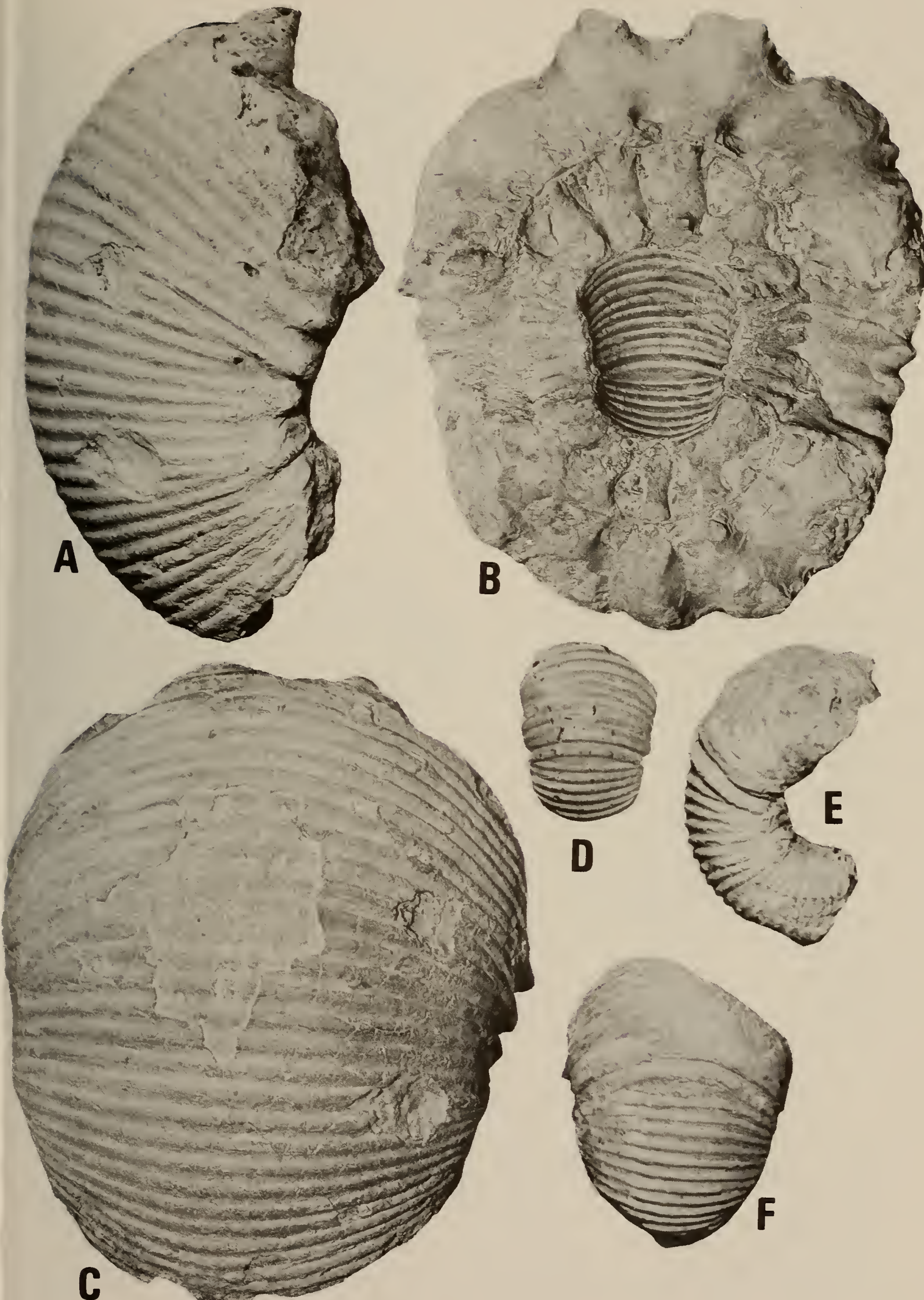

Fig. 71. *Olcostephanus* (*Olcostephanus*) *rogersi* (Kitchin) (♀), × 0,44. A–D. Lateral, dorsal, and ventral views, and ventral view of a plasticine mould of the internal whorls of SAM–PCU1542. E–F. Lateral and ventral views of PEM–1468/81, an immature macroconch.

Fig. 72. *Olcostephanus* (*Olcostephanus*) *rogersi* (Kitchin) (♀). The holotype of *Rogersites modderensis* (Kitchin), BM–C32201. × 0,75.

ribs become almost radial. From the umbilical bullae, bundles of three, very rarely only two, radial secondaries pass straight across the venter, although on the adoral portion of the body chamber, i.e. with the egression of the umbilical seam, they become distinctly prorsiradiate. There is a deep oblique parabola about 180° from the peristome, the adapical rib of which is prominently flared. The peristome is virtually identical to this parabola except that the posterior margin is even more prominently flared, while the adoral rib bears well-preserved lateral lappets which have a subhorizontal twist to them.

Macroconch (♀): in the slightly crushed holotype of *O. modderensis* (Kitchin) (Fig. 72), which represents merely the inner whorls of the macroconch of this species, well-developed rursiradiate primary ribs terminate in about 16 sharp umbilical bullae on the outer whorl. These give rise to bundles of commonly 3, occasionally 4, very coarse, radial secondaries, generally with an intercalated rib between bundles. The secondary ribbing may become slightly prorsiradiate as a parabola is approached. There is a very prominent, deep, oblique parabola on the outer whorl.

The following is a description of the holotype of *O. kitchini* (Spath) based on a plastotype supplied by M. K. Howarth: the shell is gigantic, extremely inflated, with a very depressed whorl section. The umbilical seam of the outer whorl has already begun to egress, showing it to represent part of the body chamber. The umbilicus is narrow and very deep. The umbilical walls of the penultimate whorl are very steep, convex, and ornamented with 17 prominent rursiradiate primaries which begin at, or close to, the umbilical seam and terminate in prominent bullae on the umbilical shoulder. On the final whorl

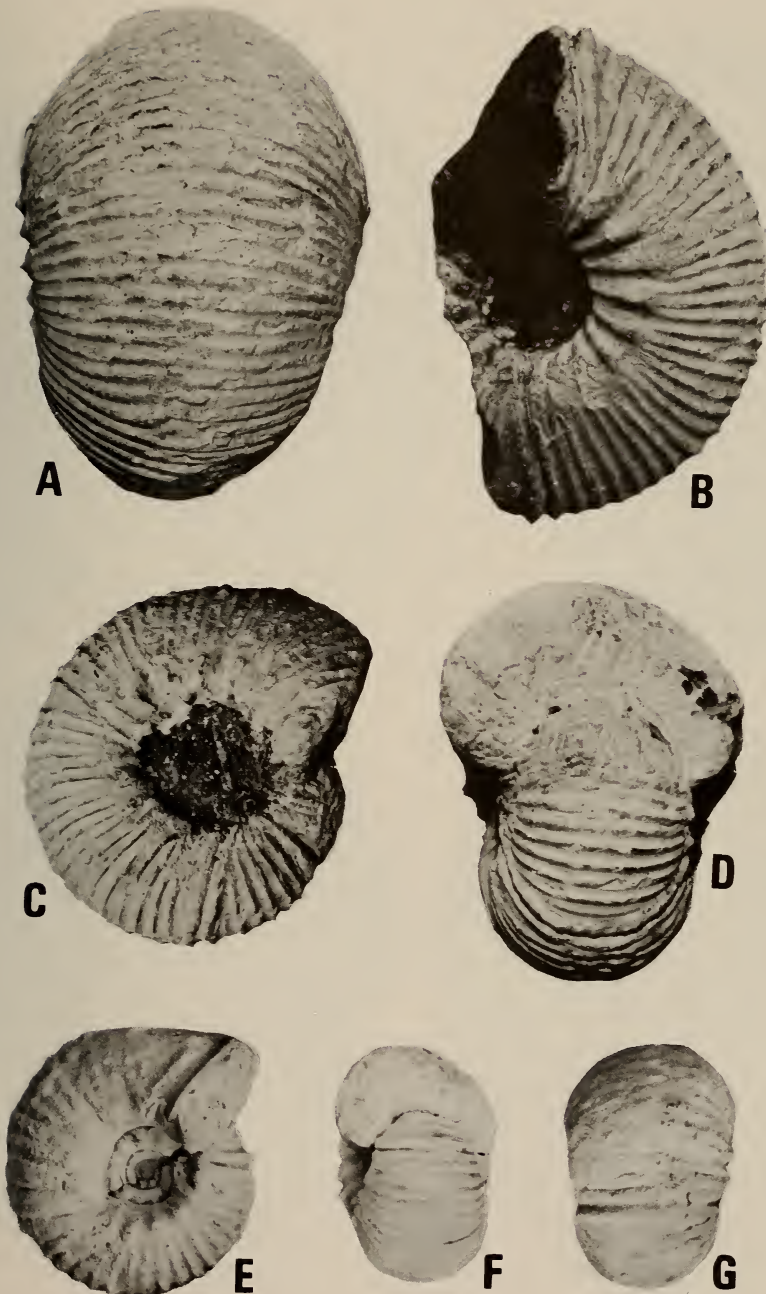

Fig. 73. *Olcostephanus* (*Olcostephanus*) *rogersi* (Kitchin) (♀). A–B. Ventral and lateral views of AAS–989e, × 0,75. C–D. Lateral and front views of AAS–370, a specimen which is only tentatively included here, × 0,75. E–G. Lateral, front and ventral views of a juvenile in the Albany Museum, × 1.

Fig. 74. A, C. *Olcostephanus* (*Olcostephanus*) *rogersi* (Kitchin) (♀). Lateral and ventral views of SAM–5070, × 0,44. B, D. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe) (♀). Lateral and ventral views of PEM–1463/41. Note the rapid rate of inflation, × 0,44.

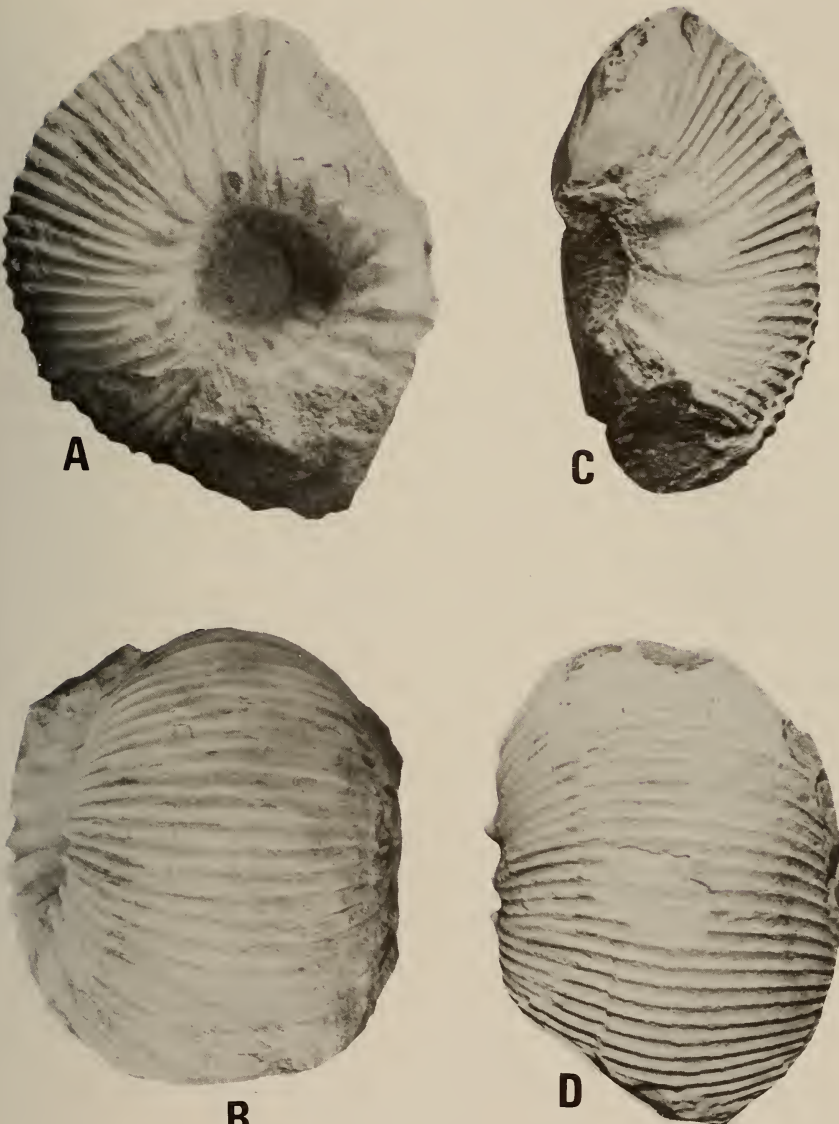

Fig. 75. A–B. *Olcostephanus* (*Olcostephanus*) *rogersi* (Kitchin) (♀). Lateral and ventral views of a specimen in the Geological Survey, Pretoria, × 0,75. C–D. *Olcostephanus* sp. Lateral and ventral views of a macroconch fragment which approaches *O. saintoursi* (Collignon), but appears to lack constrictions, SAM–PCU1562. × 0,44.

Fig. 76. *Olcostephanus* (*Olcostephanus*) *rogersi* (Kitchin) (♂). Whorl section of the holotype. × 1.

the bullae become rounded and swollen, and very prominent, while the primaries weaken considerably on the umbilical wall, being almost entirely effaced on the adoral portion of the outer whorl. Extremely coarse secondaries arise from the umbilical tubercles and vary from almost radial to slightly prorsiradiate in direction. There are commonly 3 secondary ribs per tubercle, with an intercalated rib between bundles, although on the adoral portion of the outer whorl there are commonly 4 ribs per bundle. There is not the slightest doubt that this species merely represents a mature growth stage of *O. modderensis*.

Measurements

No.	D	H	Wi	W/H	Uo	Ui
PEM–1468/81	85	32	?	?	41	28 (33) (♀)
,,	75	28	55	1,96	29	?
,,	55	23	37	1,61	21	8 (15)
Plastotype of *O. modderensis*	77	38	59	1,55	25	? (♀)
	65	28	50	1,79	21	10 (15)
SAM–PCU1542	*c.* 220	75	155	2,06	?	? (♀)
,,	*c.* 125	?	84	?	?	?
,,	*c.* 60	?	45	?	?	?
SAM–5070	*c.* 170	77	119	1,55	85	45 (26) (♀)
,,	*c.* 140	60	?	?	65	?
LJE–989e	75	28	48	1,71	27	13 (17) (♀)
,,	54	33	35	1,52	20	12 (22)
SAM–5071	58	24	35	1,46	26	16 (28) (♂)
,,	46	26	30	1,50	21	11 (24)
,,	35	15	24	1,60	18	?
LJE–989b	59	17	30	1,76	27	16 (27) (♂)
,,	47	15	29	1,93	19	11 (23)
,,	33	11	22	2,00	15	7 (21)
Plastotype of *O. kitchini*	235	90	*c.*195	2,17	95	69 (29) (♀)

Discussion

The only significant difference between the holotypes of *O. modderensis* and *O. rogersi* is the extreme inflation of the former and consequently they are regarded as sexual dimorphs.

In 1930, Spath, when describing *Rogersites kitchini*, referred to a large but fragmentary specimen which he considered '. . . closer to the present species (*R. kitchini*) than to any other described form of *Rogersites*', while considering it to have '. . . the general appearance of what a gigantic *R. schenki* may be supposed to be like' (Spath 1930: 149). This specimen, SAM–5070, is here figured (Fig. 74A, C) and can be seen to show all the characteristics of *O. rogersi* (♀). It is still septate at a diameter of 175 mm and thus represents merely the inner whorls of a much larger specimen. It has rursiradiate primary ribs terminating in umbilical bullae on the umbilical shoulder, from which arise 3–4 radial secondaries. At this diameter there are 14 secondary ribs per 4 bullae. A prominent deep parabola is evident at a diameter corresponding to about 130 mm. There seems little doubt that this example represents merely a larger growth stage than that represented by the holotype of *O. modderensis*.

Another gigantic phragmocone (Fig. 71A–C), approximately 220 mm in diameter, shows an even later growth stage in the ontogeny of this species. The secondary ribbing is still remarkably coarse, with 3–4 radial secondaries arising from each umbilical bulla and 17 secondaries per 4 bullae on the outer whorl. The umbilicus is narrow and very deep, with broad, almost vertical, slightly convex umbilical walls ornamented with prominent rursiradiate primaries. Whilst the outer whorl, admittedly not complete, shows no sign of parabolae, an impression of an inner whorl corresponding to a diameter of about 60 mm shows a deep, oblique parabola, and at this growth stage would appear to be almost identical to the holotype of *O. modderensis*. On the adoral portion of the outer whorl of this specimen the umbilical bullae are seen to become more prominent, a trend which is continued in the even larger, approximately 300 mm diameter, holotype of *O. kitchini* (Spath), a species which is undoubtedly conspecific with the present form.

Kitchin (1908) noted a slight forward inclination of the secondary ribbing on the adoral portion of the outer whorl of *O. modderensis*, but thought it might have been due to crushing. However, the habit of the ribbing becoming prorsiradiate as it approaches the peristome, and thus also parabolae (which are interpreted as relict peristomes), is common to many species of *Olcostephanus*. Indeed, *O. tenuicostatus* Imlay, a synonym of *O. atherstoni*, was distinguished by '. . . the forward inclination of the ribs near the aperture' (Imlay 1937: 562).

Olcostephanus rogersi is undoubtedly closely related to *O. baini* (Sharpe), as is evidenced by the close similarity of the microconchs. *Olcostephanus baini* (♂) differs from *O. rogersi* (♂) in having slightly fewer secondaries per bulla, while the direction of ribbing is prorsiradiate and not radial as in *O. rogersi*. A subtle, but distinctive difference is also seen in the nature of the whorl sections, that of *O. rogersi* (♂) being more depressed, with a broader, flatter

Fig. 77. *Olcostephanus* (*Olcostephanus*) *angusticoronatus* (Imlay) (♀). The holotype from the Taraises Formation of northern Mexico (after Imlay 1938). × 1.

venter, whereas the whorl section of *O. baini baini* (♂) is almost semicircular. Kitchin (1908) considered the weak umbilical tubercles of *O. rogersi* important in the separation of this species from *O. baini* but this feature is due to the fact that the holotype is an internal mould.

Olcostephanus baini var. *sphaeroidalis* (Spath) (♂) has a less inflated form while the secondary ribbing is also prorsiradiate. Whilst the differences between *O. rogersi* and *O. baini* may seem slight, the very marked differences between the macroconch forms of these two species suggests that the separation is a valid one.

In describing the ammonite fauna of the Taraises Formation of northern Mexico, Imlay (1938) created the new species *Valanginites angusticoronatus* (Fig. 77) for very involute, globose forms with rursiradiate primary ribs terminating in 16 umbilical bullae from which radiate bundles of 3–4 ribs. There are two prominent parabolae per whorl. This species is very close to the inner whorls of *O. rogersi* macroconch from which it appears to differ in being somewhat more involute and more finely ribbed.

Although originally assigned to the.genus *Holcostephanus*, '*H.*' *bachelardi* Sayn (Fig. 78) has recently been included in the synonymy of *Valanginites psaephoides* (Mayer–Eymar) (Thieuloy 1977*a*).

Olcostephanus imbricatus (Baumberger) (Fig. 79) is a strongly inflated, globose species with coarse almost radial secondary ribs which arise from 19–20 umbilical bullae. According to Baumberger (1908: 17), the secondaries arise in pairs from the bullae but quickly bifurcate so that 4 ribs from each bulla cross the venter. There are prominent parabolae on the inner whorls. This species is very close to the macroconch of *O. rogersi* and this relationship bears closer scrutiny.

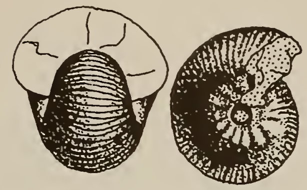

Fig. 78. *Valanginites psaephoides* (Mayer-Eymar). The holotype, by monotypy, of *Holcostephanus bachelardi* Sayn allegedly from the Barremian of France (after Sayn 1889). × 1.

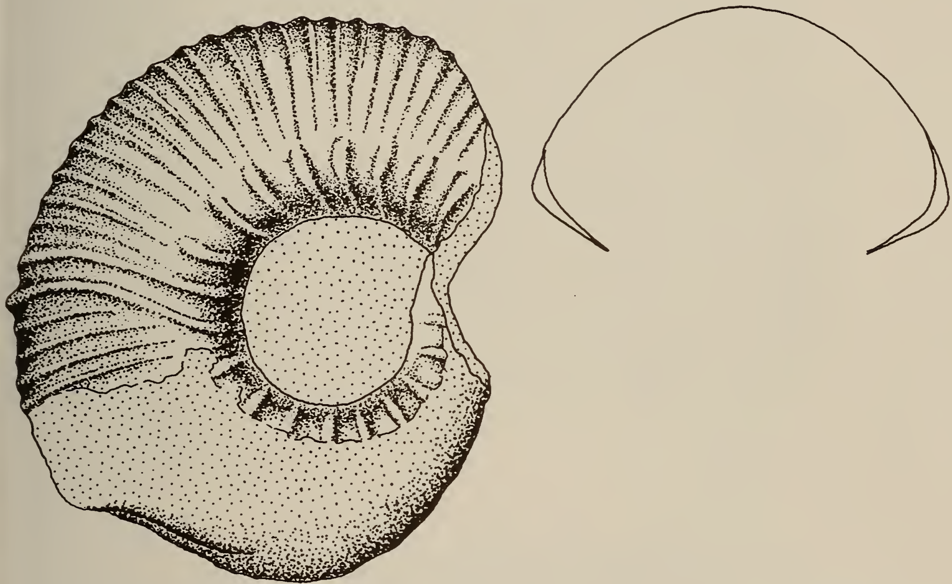

Fig. 79. *Olcostephanus* (*Olcostephanus*) *imbricatus* (Baumberger) (♀). A hypotype from the Swiss Jura (after Baumberger 1908). × 1.

The resemblance between *O. crassicostatus* (Spath) (Fig. 80) and the *O. baini* microconch was first noted by Kitchin (1908) when he described the former as *Holcostephanus* cf. *baini* (Sharpe). The large number of *O. baini* microconchs now available allows a better judgement of the intraspecific variation within this dimorph, and hence a closer comparison with *O. crassicostatus*. The latter species differs from *O. baini* (♂) in its larger adult size, generally radial secondary ribbing although, as in most species of *Olcostephanus*, this tends to become prorsiradiate near the aperture, and in commonly having three secondary ribs arising from each bulla. In addition, the whorl section of *O. crassicostatus* is strongly depressed and with a broad, flattish, gently rounded venter. The features which separate *O. crassicostatus* from *O. baini* are all characters typical of the *O. rogersi* microconch and hence *O. crassicostatus*

Fig. 80. *Olcostephanus* (*Olcostephanus*) *rogersi* (Kitchin) (♂). The holotype of *Rogersites crassicostatus* Spath, SAM–4698, a gerontic microconch. × 1.

is considered to be based upon a gerontic individual of *O. rogersi* (♂). Two other individuals, SAM–PCU1527 and PEM–1463/42, show these same features, the former at 72 mm diameter and with the peristome and lappets preserved and the latter preserved as an internal mould.

'*Subastieria*' *chanchelula* (Anderson 1938) shows a depressed reniform whorl section, with a deep, narrow umbilicus and steep umbilical walls. Prorsiradiate primaries terminate in bullae on the umbilical shoulder from which arise 2–3 rectiradiate secondaries with an occasional intercalated rib between bundles. Parabolae appear to be lacking. The absence of parabolae and the prorsiradiate primary ribs serve to distinguish this species from *O. rogersi*. According to Imlay (1960) it may be a juvenile *Simbirskites*.

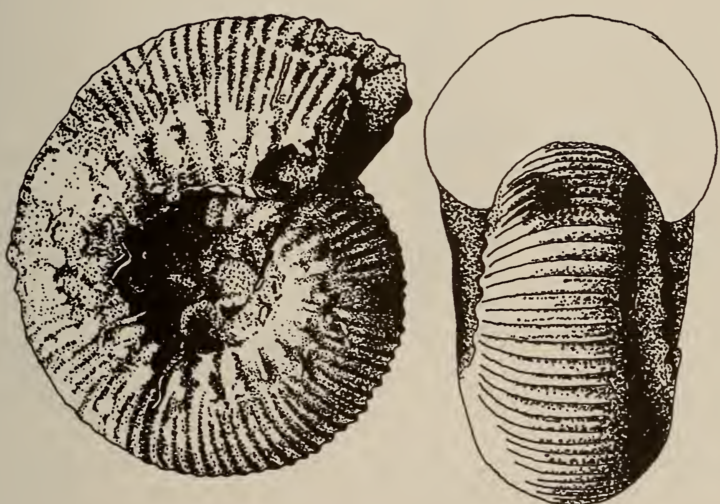

Fig. 81. *Olcostephanus* (*Olcostephanus*) *radiatus* Spath. The holotype from the Spiti Shales of Pakistan (after Spath 1939). × 1.

Olcostephanus radiatus Spath (Fig. 81) is very close to *O. rogersi* (♂) but differs in having more umbilical bullae (twenty-four) and, in the holotype, by the absence of parabolae.

Olcostephanus madagascariensis (Lemoine) (Fig. 14), the type of the subgenus *Lemurostephanus*, resembles the *O. rogersi* microconch but can be distinguished by having distinctly sloping umbilical walls and more numerous bullae. The specimen figured by Fatmi (1977: 271, pl. 5 (fig. 4)) is indistinguishable from the present material of *O. rogersi* (compare Fatmi's specimen with Figure 70A–C), and is included in the synonymy of the latter species. *Olcostephanus mitreanus* (d'Orbigny) (Fig. 17), which includes amongst its synonyms *O. detonii* (Rodighiero) (Fig. 15), *O. wynnei* Spath (Fig. 16), and possibly the specimen figured by Thieuloy (1977*a*, pl. 9, fig. 27) as *O.* (*Lemurostephanus*) aff. *sanctifirminensis* Thieuloy, differs from *O. rogersi* (♂) in being more evolute.

Fig. 82. *Olcostephanus* (*Olcostephanus*) *leanzai* (Giovine) (♀). The holotype from the Lower Hauterivian of Neuquén, Argentina (after Giovine 1950). × 0,66.

'*Maderia*' *multituberculata* Imlay (1938) is based upon an inflated, globose, pyritic nucleus with a strongly depressed, semilunate whorl section. About 26 rursiradiate primary ribs terminate in bullae on the umbilical wall and give rise to 2–3 prorsiradiate secondary ribs. Parabolae are prominent and thinning of the ribs across the siphonal line is insignificant. This species differs from *O. rogersi* in its more numerous primary ribs and prorsiradiate secondaries. It is probably based upon the innermost whorls of *O. globosus* Spath.

Olcostephanus leanzai (Giovine) (Fig. 82) is a coarsely ribbed, globose species which was compared with *O. rogersi* and *O. modderensis*. It is unknown whether the inner whorls of this species bear parabolae. So far as can be judged, it differs from the *O. rogersi* macroconch only in the possession of more numerous umbilical bullae but the differences are slight.

Olcostephanus saintoursi (Collignon) (Fig. 83) is too fragmentary to allow a proper comparison, but has finer, more numerous secondaries and is apparently from Lower Valanginian strata. The large size and strong inflation

Fig. 83. *Olcostephanus* (*Olcostephanus*) *saintoursi* (Collignon) (♀). The holotype from the Upper Valanginian of Madagascar (after Collignon 1962). × 1.

of this species clearly indicate it to be an immature macroconch but topotype material is necessary to prove its validity.

Dobrodgeiceras wilfridi (Karakasch) (Fig. 12) is another strongly inflated form but differs from the *O. rogersi* macroconch in its small adult size, extremely narrow umbilicus, and the shifting of the umbilical tubercles to a ventrolateral position with a consequent lengthening of the primaries.

Olcostephanus laticostus (Gerth) (Fig. 47) has swollen umbilical tubercles and lacks parabolae and hence cannot be confused with *O. rogersi*. It is, how-

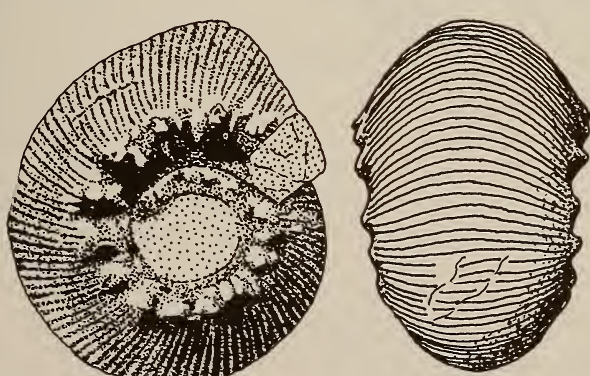

Fig. 84. *Olcostephanus* (*Olcostephanus*) *singularis* (Baumberger). The holotype, by monotypy, of *Holcostephanus klaatschi* Wegner, from the Lower Hauterivian of Basses-Alpes, France (after Wegner 1909). × 1.

ever, close to *O. klaatschi* (Wegner) (Fig. 84) from which it differs in the possession of much coarser ribbing. Wegner's (1909) species differs from *O. rogersi* in being more finely and densely ribbed, lacking parabolae, and with swollen umbilical tubercles at early growth stages. It is almost certainly merely based upon the inner whorls of *O. singularis* (Baumberger).

Astieria dolioliformis Roch (Fig. 13) was erected for extremely inflated, globose forms with a very narrow umbilicus ornamented with nineteen primaries, each terminating in a small umbilical tubercle. Each bulla gives rise to two secondary ribs separated by an intercalatory. As suggested by Spath (1939: 25), this species is best assigned to the genus *Valanginites*.

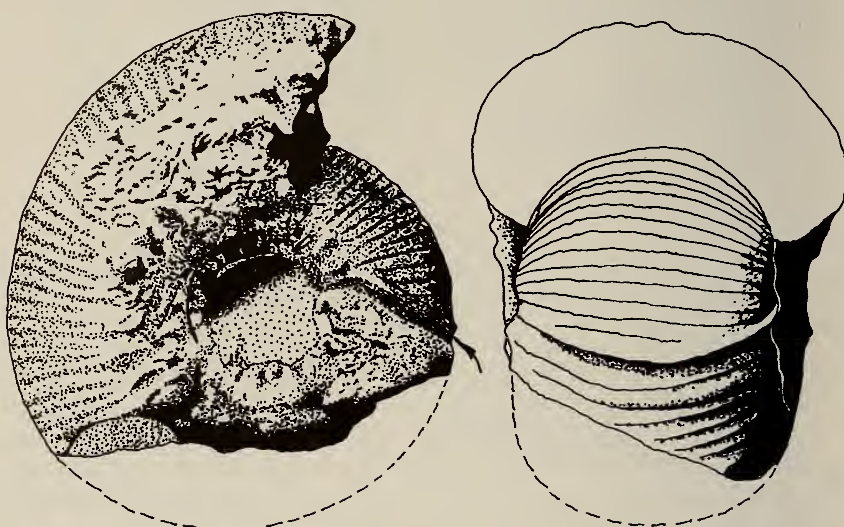

Fig. 85. *Olcostephanus* (*Olcostephanus*) *globosus* Spath (♀). The holotype of *Olcostephanus pachycyclus* Spath from the Spiti Shales of Pakistan (after Spath 1939). × 1.

Olcostephanus pachycyclus (Folgner MS) Spath (Fig. 85) is very close to the holotype of *O. modderensis*, i.e. the *O. rogersi* macroconch, from which it differs only in the possession of far more umbilical bullae (twenty-three at 70 mm diameter). Fatmi (1977) has included this species in the synonymy of *O. globosus* Spath (Fig. 86).

Olcostephanus drumensis (Sayn MS) (Kilian) (Fig. 87) differs from *O. rogersi* in the possession of more numerous umbilical tubercles and in its denser, finer secondary ribbing.

Olcostephanus psilostomus quadricostatus (Tzankov) (Fig. 88) was based upon two individuals, a macroconch and a microconch. The latter is herein selected as lectotype and seems very close to *O. mitreanus* (♂), although it is unclear from Tzankov's (1943) figure if the Bulgarian form has parabolae. It differs from the *O. rogersi* microconch in its smaller adult size, wider umbilicus

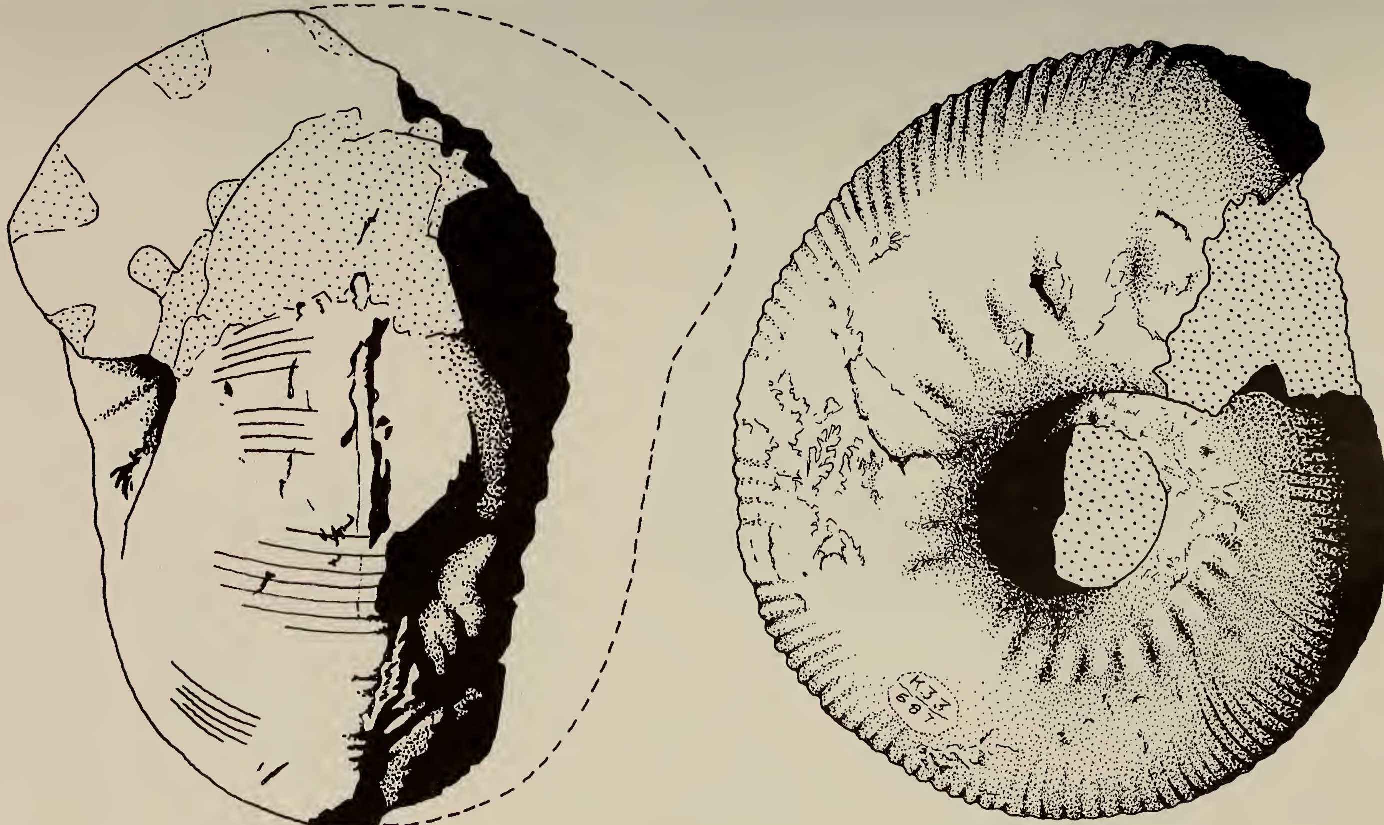

Fig. 86. *Olcostephanus* (*Olcostephanus*) *globosus* Spath (♀). The holotype from the Spiti Shales of Pakistan (after Spath 1939). × 1.

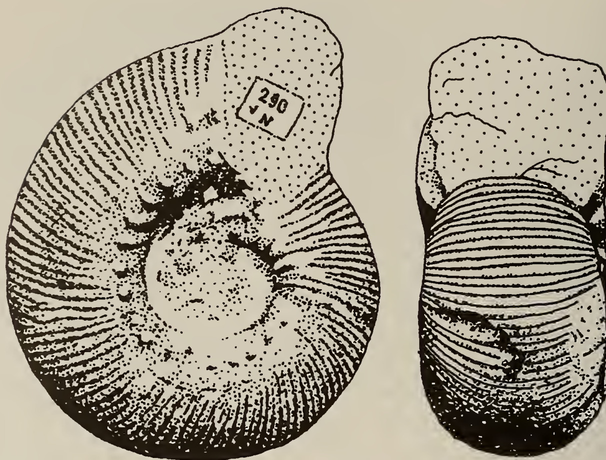

Fig. 87. *Olcostephanus* (*Olcostephanus*) *drumensis* (Sayn MS) Kilian. The holotype, by monotypy, from the Middle Valanginian of Fontanil, France (after Kilian 1910). × 1.

and apparent lack of parabolae. It still remains to be demonstrated that the macroconch which forms part of the syntype series is, in fact, conspecific with the microconch. Since the Bulgarian microconch is certainly specifically distinct from '*O. psilostomus*', the writer would suggest elevating Tzankov's (1943) trivial name to full specific status, i.e. *O. quadricostatus* (Tzankov).

Occurrence

This species is known with certainty only from South Africa and Pakistan, but may also be present in the Swiss Jura and Argentina.

Olcostephanus (*Olcostephanus*) *victoris* Spath, 1939 (♀)
Figs 89–90

Olcostephanus victoris Spath, 1939: 20, pl. 19 (fig. 7a–b). Fatmi, 1977: 268.

Material

A single specimen, LJE–991, from Addo Drift East B farm in the Uitenhage district.

Holotype

The original of *Olcostephanus victoris* figured by Spath (1939: 20, pl. 19 (fig. 7a only)) (Fig. 89) from the Chichali Pass of Pakistan.

Diagnosis

A rather evolute species of *Olcostephanus*, probably representing the inner whorls of a larger macroconch, with a somewhat compressed form. Primary

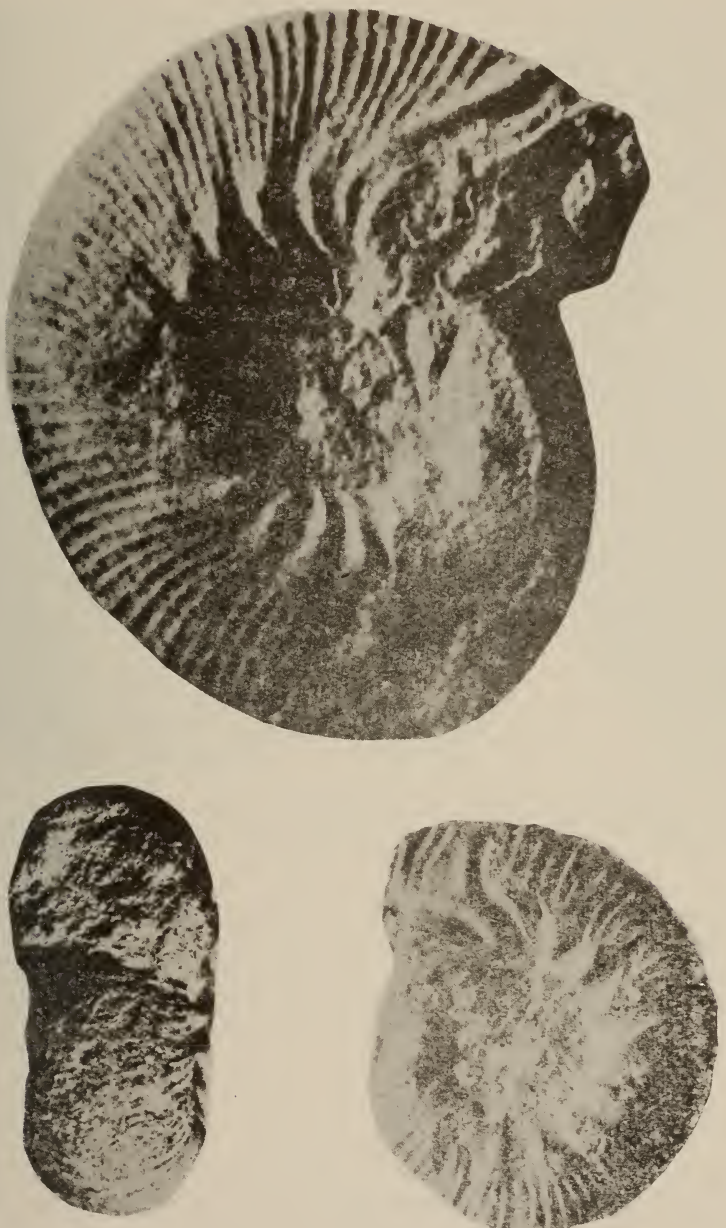

Fig. 88. *Olcostephanus* (*Olcostephanus*) *quadricostatus* (Tzankov). The syntypes from Bulgaria, of which the smaller specimen, a microconch, is selected as lectotype (after Tzankov 1943). × 1.

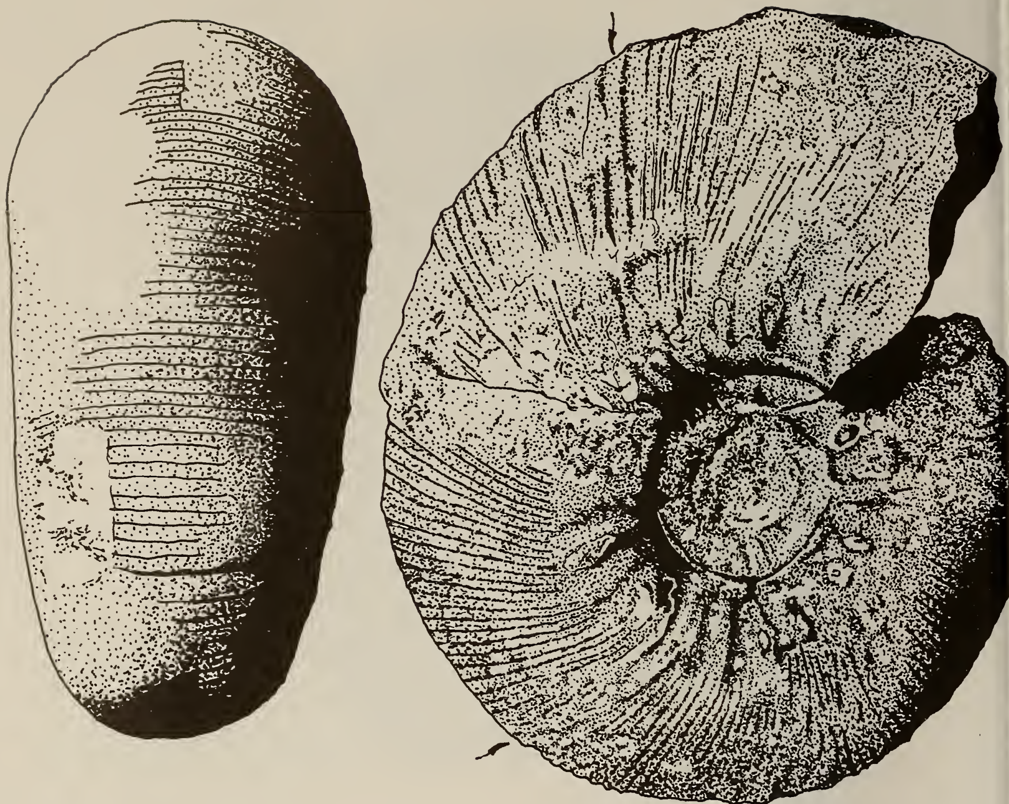

Fig. 89. *Olcostephanus* (*Olcostephanus*) *victoris* Spath (♀). Lateral view of the holotype and ventral view of a paratype, from the Spiti Shales of Pakistan (after Spath 1939). × 1.

ribs rursiradiate, terminating in about 28 umbilical bullae on the outer whorl, from which arise bundles of 3–4 fine, prorsiradiate secondaries. Whorl section suboval, depressed. Parabolae present. Umbilical shoulder rounded, with maximum width some way above the umbilical shoulder.

Description

A single entirely septate specimen (Fig. 90) from the Sundays River is assignable to Spath's species.

This example, LJE–991, has recrystallized test preserved. The shell is somewhat inflated and rather evolute, with a strongly depressed whorl section. At 120 mm diameter the specimen is entirely septate and thus almost certainly represents the inner whorls of a larger probably compressed macroconch. The umbilicus is rather wide and moderately deep, with steep umbilical walls and a well-rounded umbilical shoulder. The venter is rather broad and flattish, but evenly rounded.

On the adoral one-quarter of the outer whorl there is already a distinct egression of the umbilical seam, so that a short distance of secondary ribbing is visible on at least the penultimate whorl. Primary ribs begin at the umbilical seam and pass backwards (rursiradiate) to 26 rather inconspicuous bullae on the umbilical shoulder. These in turn give rise to bundles of 3–4 fine, prorsiradiate secondaries, commonly with an intercalated rib between bundles. The secondaries recurve slightly so as to cross the venter transversely. There are 25 secondaries per 6 bullae on the outer whorl, with 15 ribs within a 50 mm distance along the venter. Maximum width is some way above the umbilical bullae. There are two prominent parabolae on the outer whorl, with a third partially hidden by the adoral portion of the outer whorl.

Fig. 90. *Olcostephanus victoris* Spath (♀). Lateral, front and ventral views of LJE–991. Note the convex flanks and the egression of the umbilical seam at a stage when the shell is still entirely septate. × 0,44.

Measurements

No.	D	H	Wi	W/H	Uo	Ui
LJE–991	115	41	69	1,68	51	30 (26)
,,	95	38	56	1,47	42	23 (24)
,,	64	30	37	1,23	26	16 (25)

Discussion

The Uitenhage example closely resembles Spath's holotype. The latter does not, however, show the characteristic egression of the umbilical seam on the outer whorls. None the less, it represents an earlier growth stage than the present specimen and thus may well have become more evolute with ontogeny. Fatmi (1977) considered *O. victoris* a synonym of *O. sakalavensis* Besairie but it differs from that species in being somewhat more evolute, with maximum width somewhat above the umbilical tubercles and in possessing constrictions.

Olcostephanus uitenhagensis (Kitchin) also becomes markedly evolute on the final whorl, hence at a much later stage than *O. victoris*, whilst its inner whorls are more compressed, with broader, flatter flanks. It is unknown whether the inner whorls of *O. uitenhagensis* bear parabolae.

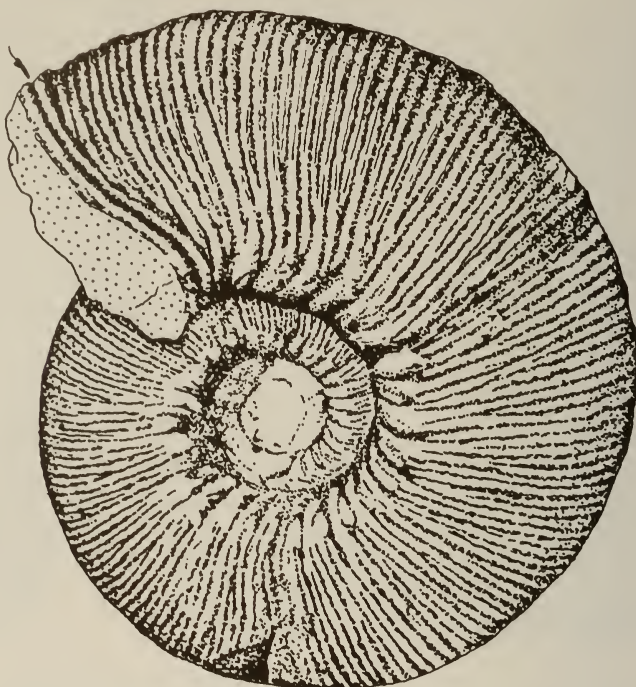

Fig. 91. *Olcostephanus* (*Olcostephanus*) *schafarziki* (Somogyi) (♀). The holotype from Martonkút (after Somogyi 1916). × 1.

Olcostephanus schafarziki (Somogyi) (Fig. 91) would also appear to be rather evolute at moderate diameters but differs from *O. victoris* in lacking parabolae and in the frequent bifurcation of secondaries. In this respect it closely resembles *O. irregularis* (Wegner), with which it may well be conspecific.

Occurrence

This species is currently known only from the Sundays River Formation and the Spiti Shales of Pakistan.

Olcostephanus (*Olcostephanus*) *fascigerus* Spath, 1939 (♀)

Figs 92–97

Holcostephanus (*Astieria*) cf. *convoluta* von Koenen, Uhlig, 1903: 394, pl. 78 (fig. 1).
Olcostephanus fascigerus Spath, 1939: 18, pl. 4 (figs 1–3). Fatmi, 1977: 268, pl. 3 (fig. 3).
Holcostephanus uhligi Collignon, 1962: 23, fig. 827.

Material

Four adult macroconchs, SAM–PCU1568, 1611, SAM–5074, BM–C7126.

Holotype

The original of the specimen figured by Spath (1939: 18, pl. 14 (figs 1–3)) and here refigured (Fig. 92) from the top bed of the middle member of the Chichali Formation of northern Pakistan.

Diagnosis

Large inflated cadicone macroconchs (+ 150 mm diameter), with a depressed whorl section and evenly rounded venter. Between 18 and 22 prominent umbilical bullae on the final whorl give rise to 4–5 radial to prorsiradiate, fine, flexuous, secondary ribs, occasionally bifurcating or with intercalatories, and with 2–5 intercalated ribs between bundles. Parabolae lacking at all growth stages and with a simple peristome in maturity.

Description

The material assigned to this species comprises large, inflated cadicones with depressed whorls and subquadratic whorl sections. Characteristic are the distinct flanks which merge into the broad, evenly rounded venter and provide the whorl section with its subquadrate appearance. The rursiradiate primaries terminate on the umbilical shoulder in about 20–22 somewhat bullate, very prominent tubercles which generally give rise to 5, less commonly 4 or 6, almost radial (SAM–PCU1611) to prorsiradiate (BM–C47126) fine secondaries, usually with 3 intercalatories between bundles. Another feature which distinguishes this species from all other macroconchs from the Uitenhage Group is the almost constant width of the final whorl, which tends to give the shell a cylindrical aspect when viewed ventrally.

In a second specimen, SAM–5074 which shows the same prominent umbilical bullae and cylindrical form as SAM–PCU1611, the secondary ribbing on the adoral portion of the body chamber is very fine and thread-like, with fine secondaries occurring intercalated high up on the flanks.

On SAM–PCU1611 there are 23 secondaries per 3 bullae on the outer whorl, with 18 secondaries within a 100 mm distance along the venter. On the adoral portion of the body chamber the secondary ribbing becomes distinctly prorsiradiate.

Measurements

No.	D	H	Wi	W/H	Uo	Ui
SAM–PCU1611	226	70	111	1,59	115	?
SAM–5074	235	78	110	1,41	85	?
,,	165	75	100	1,33	65	?
BM–C47126	215	100	121	1,21	88	62 (29)

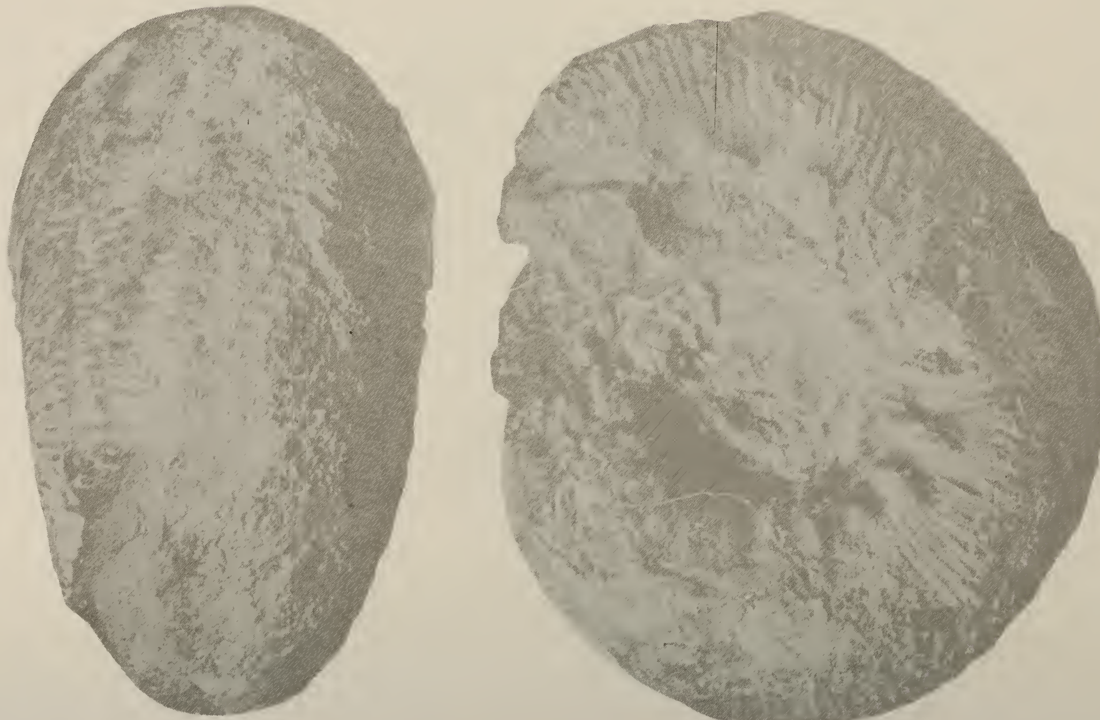

Fig. 92. *Olcostephanus* (*Olcostephanus*) *fascigerus* (Spath) (♀). The holotype from the Upper Valanginian Spiti Shales of Pakistan (after Spath 1939). × 1.

Fig. 93. *Olcostephanus* (*Olcostephanus*) *fascigerus* Spath (♀). Lateral view of the holotype of *Holcostephanus uhligi* Collignon (after Uhlig 1903). × 1.

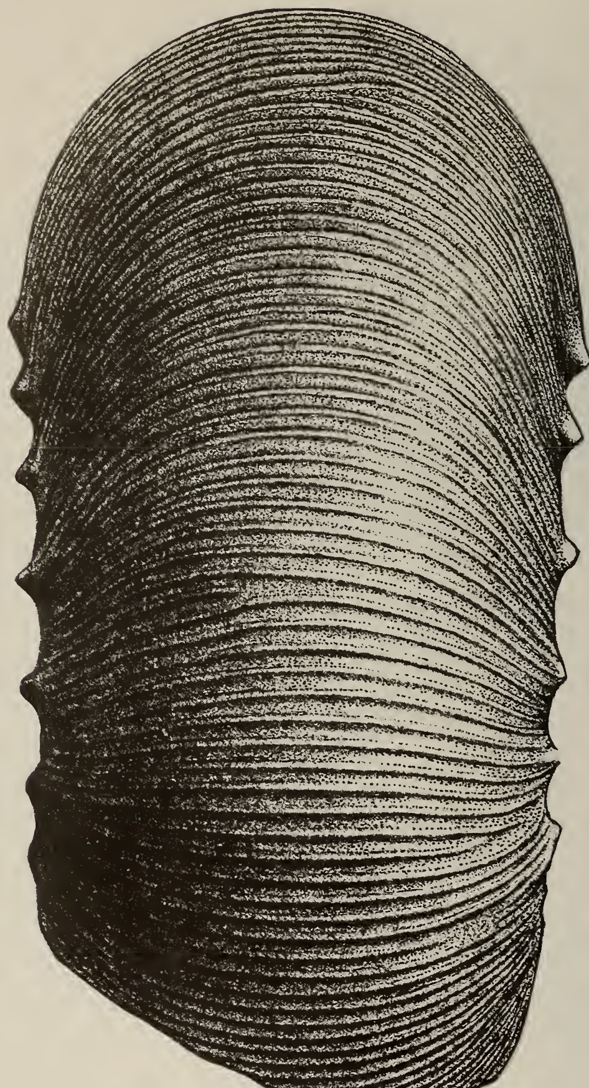

Fig. 94. *Olcostephanus* (*Olcostephanus*) *fascigerus* Spath (♀). Ventral view of the holotype of *Holcostephanus uhligi* Collignon (after Uhlig 1903). × 1.

Fig. 95. *Olcostephanus* (*Olcostephanus*) *fascigerus* Spath (♀). Ventral and lateral views of SAM–PCU1611. Note fine secondaries, prominent bullae and constant rate of inflation. × 0,44.

Fig. 96. *Olcostephanus* (*Olcostephanus*) *fascigerus* Spath (♀). Ventral and lateral views of BM–C47126, a specimen with fewer umbilical bullae than the holotype. × 0,44.

Fig. 97. *Olcostephanus* (*Olcostephanus*) *fascigerus* Spath (♀). Ventral and lateral views of SAM–PCU1611. × 0,44.

Discussion

The writer would agree with Spath (1939: 19) that this species should include the adult figured by Uhlig (1903: 394, pl. 78 (fig. 1)) as *Holcostephanus* (*Astieria*) cf. *convoluta* von Koenen (Figs 93–94). Since, however, Uhlig's specimen was subsequently made the type of the new species *H. uhligi* Collignon, the latter name becomes a junior subjective synonym of *O. fascigerus*.

Although Spath (1939) and Fatmi (1977) mention constrictions in their discussions of *O. fascigerus*, none of the figured material shows parabolae and it is herein assumed that parabolae are lacking in the present interpretation of this species.

Olcostephanus fascigerus can be distinguished from all other macroconch dimorphs occurring in the Sundays River Formation by the weak inflation of the whorls which provides it with a cylindrical aspect in ventral view, its prominent umbilical bullae and its fine, irregular secondary ribbing.

Occurrence

This species is at present recorded only from northern Pakistan, Madagascar, and South Africa.

Olcostephanus (*Olcostephanus*) aff. *durangensis* (Cantu Chapa) (♂)
Figs 99–100

Hoplites symonensis Böse, 1923: 96, pl. 5 (figs 5–16).
Taraisites durangense Cantu Chapa, 1966: 16.

Material

Two microconchs, SAM–PCU1547, 1549, collected in the Algoa Brick & Tile quarries at Coega (see Fig. 1).

Fig. 98. *Olcostephanus* (*Olcostephanus*) *durangensis* (Cantu Chapa). The syntypes from the Taraises Formation of northern Mexico, of which the smaller specimen is herein selected as lectotype (after Böse 1923). × 1.

Holotype

By lectotype designation herein, the smaller and more complete of the two individuals figured by Böse (1923) and here refigured (Fig. 98) from northern Mexico.

Description

In the only complete example, SAM–PCU1549, which has recrystallized test preserved, the shell is moderately inflated and involute up to the umbilical bullae, with about 80 per cent of the preceding whorl covered. However, the umbilical seam egresses noticeably on the final whorl. The umbilicus is rather wide and moderately deep, with a steep umbilical wall which becomes somewhat inclined with the egression of the umbilical seam. The umbilical shoulder is subrounded. The whorl section is semicircular, with a broadly rounded venter.

The primary ribs begin at the umbilical seam and pass strongly backwards (rursiradiate) to nineteen prominent bullae on the umbilical shoulder of the final whorl. These bullae give rise to thick, robust secondaries, almost invariably in pairs, although very occasionally there is only a single secondary rib arising from a bulla. The rib direction changes significantly on the final whorl. On the adapical portion of the outer whorl the secondaries are very slightly rursiradiate. Half-way round the final whorl the secondary ribbing has become radial, while at the peristome it is distinctly prorsiradiate. This latter feature is not, however, considered characteristic since most olcostephanids show the same tendency for the secondary ribbing to become more inclined near the peristome. There is an occasional intercalated rib between bullae. A rib which occurs intercalated on the one flank is frequently seen to arise from a bulla on the other side.

There are 15 secondaries per 6 bullae on the adoral portion of the body chamber, with 10 ribs within a 40 mm distance along the venter. Prior to the deep parabola on the outer whorl the ribbing is somewhat closer, with 6 secondaries within a 20 mm distance along the venter.

Measurements

No.	D	H	Wi	W/H	Uo	Ui
SAM–K1549	65	26	36	1,38	30	20 (31)
,,	49	21	32	1,52	23	14 (29)
SAM–K1547	45	16	25	1,56	19	12 (27)
,,	35	14	?	?	17	10 (29)

Discussion

The two Uitenhage examples are characterized by robust, distant, predominantly radial secondaries, numerous umbilical bullae, paired secondaries and semicircular whorl sections. The robust nature of the ribbing together with the prominent umbilical bullae suggests better reference to *Olcostephanus* s.s. rather than to the subgenus *Jeannoticeras* which lacks bullae and has finer, more delicate secondaries.

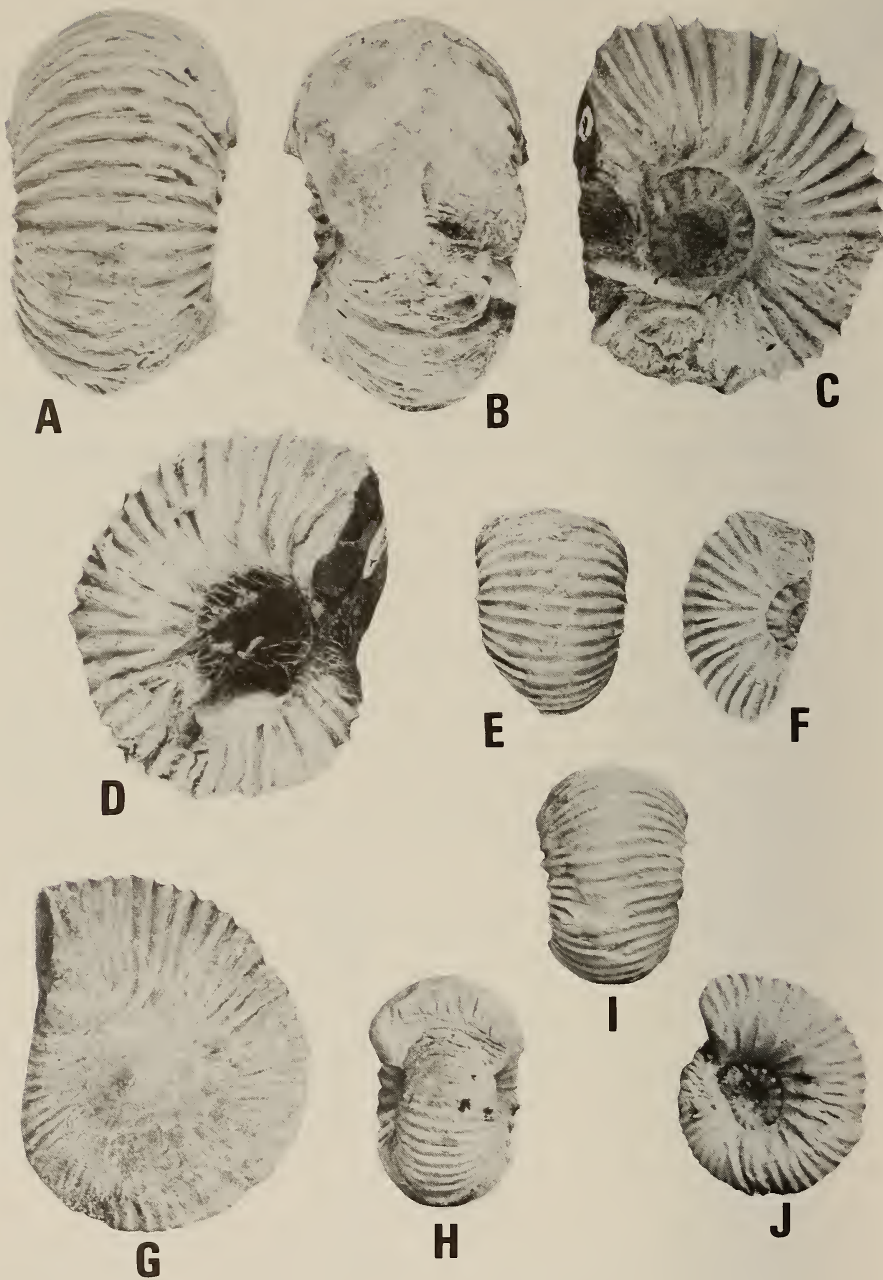

Fig. 99. *Olcostephanus* (*Olcostephanus*) aff. *durangensis* (Cantu Chapa). A–D. Ventral, front, left lateral, and right lateral views of SAM–PCU1459, a microconch, × 0,66. E–F. Ventral and lateral views of SAM–PCU1547, × 0,75. G. Lateral view of a badly crushed individual, AAS–381, × 0,66. H–J. Front, ventral and lateral views of a juvenile in the Albany Museum which may belong here, × 0,75.

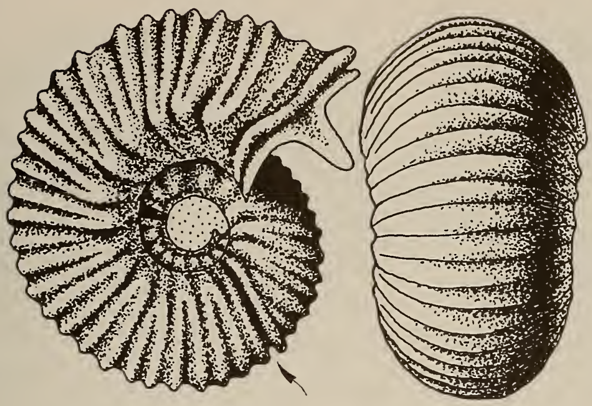

Fig. 100. *Olcostephanus* (*Olcostephanus*) aff. *durangensis* (Cantu Chapa) (♂). A reconstruction based upon SAM–PCU1549. × 1.

Olcostephanus crassicostatus (Spath) is similar, but has fewer umbilical bullae and commonly three secondaries per bulla, while *O. rogersi* (♂) has fewer, more prominent bullae, a more depressed whorl section and characteristically three secondaries per bulla.

Olcostephanus durangensis (Cantu Chapa) (Fig. 98), erected for the *Hoplites symonensis* described by Böse (1923) is very similar, but as the largest specimen is only 16,2 mm in diameter comparison is rather difficult. The Mexican species shows the characteristic radial bifurcation of coarse secondaries from the umbilical bullae, of which there are about 24 per whorl (at 16 mm diameter), but the umbilical walls of the Mexican form slope more. *Olcostephanus baini baini* (♂) has fewer umbilical bullae, from which arise 2–3 prorsiradiate secondaries.

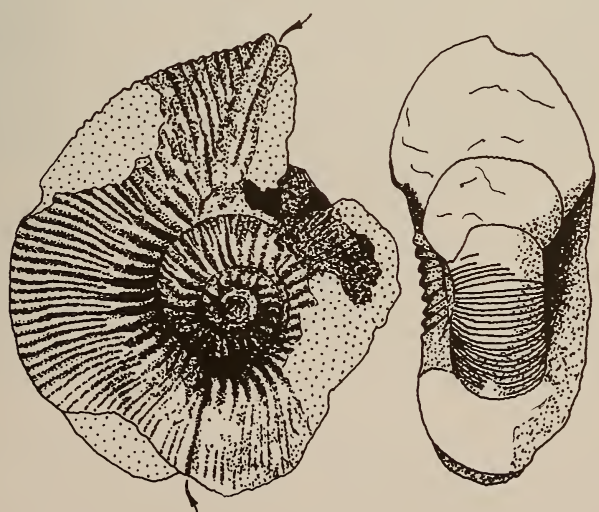

Fig. 101. *Olcostephanus* (*Jeannoticeras*) *frequens* (Zwierzycki) (♀). The holotype from the *Rutitrigonia schwarzi* Beds of Tanzania (after Zwierzycki 1914). × 1.

Fig. 102. *Olcostephanus* (*Jeannoticeras*) *frequens* (Zwierzycki) (♂). Two of the syntypes of *Astieria auriculatus* Zwierzycki from Tanzania, of which the right-hand specimen is herein selected as the lectotype (after Zwierzycki 1914). × 1.

Olcostephanus frequens (Zwierzycki) (Fig. 101), *O. auriculatus* (Zwierzycki) (Fig. 102), *O. pecki* Imlay (Fig. 103), and *O. popenoei* Imlay (Fig. 104) are all characterized by abundant primary ribs from which the secondaries commonly bifurcate and should, therefore, be included in the subgenus *Jeannoticeras*, as should *O. colorinensis* Imlay (Fig. 105). It is doubtful whether more than one species is involved in the above list.

Böse (1923) created *Hoplites aquilerae* for a juvenile form with a rather narrow umbilicus and a depressed, almost semicircular whorl section. On the outer whorl, between 27 and 28 primary ribs terminate in weak bullae on the umbilical shoulder and generally give rise to 2 prorsiradiate secondaries, with occasional intercalatories between bundles. Parabolae are apparently lacking. This species clearly belongs to the subgenus *Jeannoticeras* and differs from the present material in its much finer ribbing, more numerous umbilical bullae and the absence of parabolae.

Whiteaves (1893) introduced the species *Olcostephanus* (*Astieria*) *deansii* (Fig. 106) for a compressed form lacking parabolae and with flexuous secondary ribs which bifurcate just above the umbilical shoulder. This form is perhaps better assigned to the genus *Homolsomites*.

Olcostephanus huizachensis (Cantu Chapa) (Fig. 107) is a small, somewhat compressed species with an oval whorl section. Fifteen primaries terminate in bullae from the umbilical shoulder from which secondary ribs arise in pairs, so that there are thirty distant secondaries across the venter of the outer whorl. This species is close to the present material from which it differs in lacking parabolae and in having more distant secondaries. It is probably the microconch of *O. raricostatus* (Böse).

'*Astieria*' *neohispanica* (Böse 1923) is a very involute, compressed form with about one-quarter of the penultimate whorl visible in the umbilicus. There are about 30–35 primary ribs which seem to lack umbilical tubercles. The lower part of the flanks, immediately above the umbilical shoulder, are smooth.

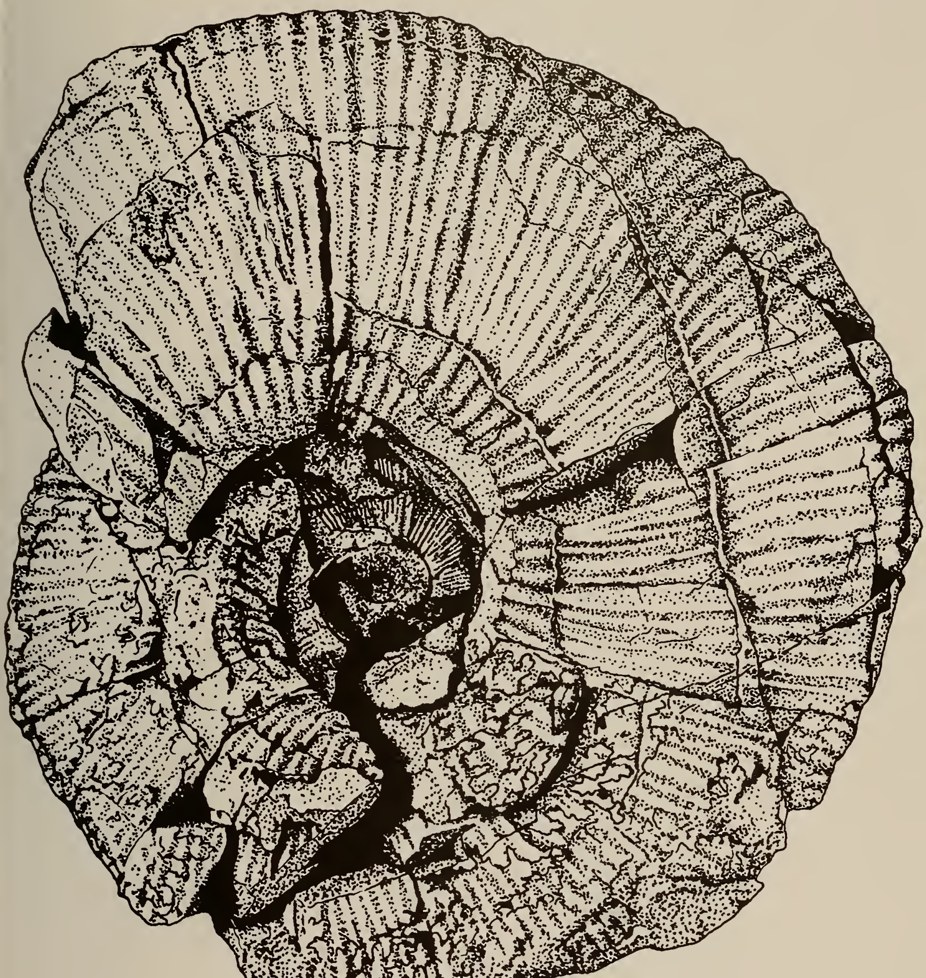

Fig. 103. *Olcostephanus* (*Jeannoticeras*) *frequens* (Zwierzycki) (♀). The holotype of *Olcostephanus pecki* Imlay from the Upper Valanginian of Oregon (after Imlay 1960). × 1.

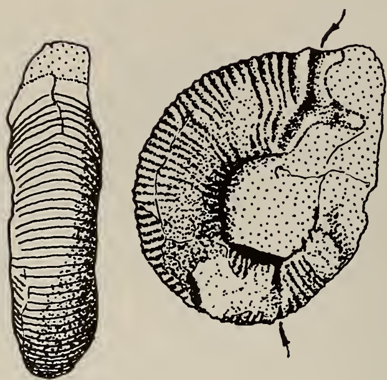

Fig. 104. *Olcostephanus* (*Jeannoticeras*) *frequens* (Zwierzycki) (♂). The holotype of *Olcostephanus popenoei* Imlay from the Upper Valanginian of Oregon (after Imlay 1960). × 1.

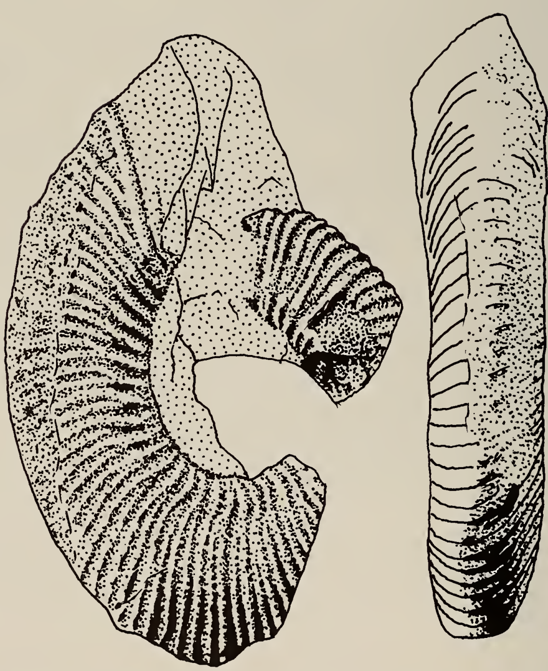

Fig. 105. *Olcostephanus* (*Jeannoticeras*) *colorinensis* Imlay (♀). The holotype from the Taraises Formation of northern Mexico (after Imlay 1938). × 1.

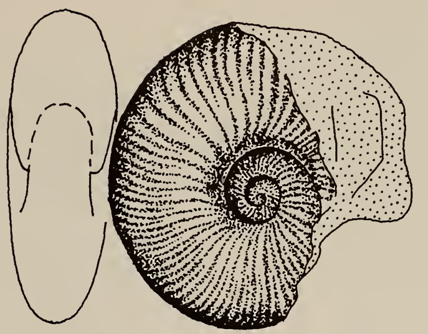

Fig. 106. *Homolsomites*? *deansii* (Whiteaves). The holotype, by monotypy, of *Olcostephanus* (*Astieria*) *deansii* Whiteaves from Queen Charlotte Island, British Columbia (after Whiteaves 1893). × 1.

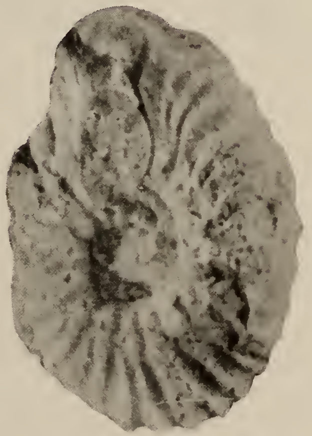

Fig. 107. *Olcostephanus* (*Olcostephanus*) *huizachensis* (Cantu Chapa) (♂). The holotype from the Taraises Formation of northern Mexico (after Cantu Chapa 1966). × 1.

Above this smooth 'periumbilical band' fine secondaries arise and occasionally bifurcate. Parabolae are lacking. In the writer's opinion, this is a species of *O.* (*Jeannoticeras*) which differs from the Uitenhage material in its much finer ribbing.

Olcostephanus elegans (Karakasch) (Fig. 108) has an inflated shell with a strongly depressed whorl section and well-rounded venter. The umbilicus is fairly wide, with sloping walls and well-rounded shoulders. There are about thirty long primaries on the outer whorl which give rise to pairs of radial secondaries with occasional intercalated ribs. This species is more finely ribbed than

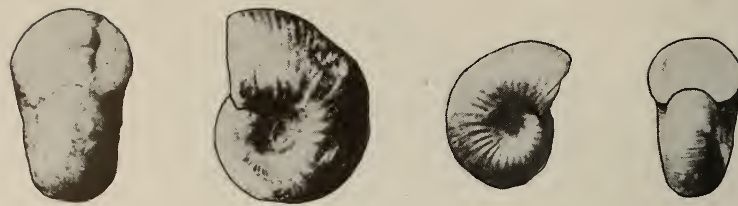

Fig. 108. *Olcostephanus* (?*Jeannoticeras*) *elegans* (Karakasch). The holotype, by monotypy, from the Upper Valanginian of the Crimea (after Karakasch 1907). × 1.

Fig. 109. *Olcostephanus*? *cadoceroides* (Karakasch). The holotype, by monotypy, from the Upper Valanginian of Crimea (after Karakasch 1907). × 1.

the present material and lacks parabolae and is undoubtedly closely related to '*Astieria*' *cadoceroides* Karakasch (Fig. 109) which seems to differ only in the presence of a thick parabolic rib on the outer whorl which is said to form two low tubercles on the venter. Whilst both these species show features of *O.* (*Jeannoticeras*), the sloping umbilical walls with prorsiradiate primaries are features of *O.* (*Subastieria*). However, the alleged ventral tubercles are not a feature of *Olcostephanus* and hence the generic classification of these two forms is uncertain.

The holotype of '*Rogersites*' *quinquestriatus* Besairie (Fig. 110) shows a subcoronate, depressed whorl section and a rather narrow umbilicus. The umbilical shoulders appear evenly rounded and seem to lack umbilical bullae. Simple rectiradiate ribs, about as wide as the interspaces, arise from the umbilical shoulder (the umbilicus is plugged with matrix) and almost invariably bifurcate above midflank, although the occasional rib remains single. There are five prominent oblique parabolae on the outer whorl. This species differs so markedly from the rather consistent characters shown by the genus *Olcostephanus* that it warrants a new generic name. In consequence, the new generic name *Jeanthieuloyites*, for Dr J. P. Thieuloy of the University of Grenoble, is proposed, with '*R.*' *quinquestriatus* Besairie (Fig. 110) as type species.

Olcostephanus bangei (Böse) (Fig. 111) is a very involute species with a narrow umbilicus and steep umbilical walls. Prominent radial primaries terminate in about 10 tubercles on the outer whorl from which arise bundles of 3–4

Fig. 110. *Jeanthieuloyites quinquestriatus* (Besairie). The holotype in the collections of the University of Paris, from the Upper Valanginian of Ambiky, Malagasy Republic. × 1.

prorsiradiate secondaries, commonly with an intercalated rib between bundles. There are 45 ribs across the venter of the outer whorl. This species differs from the present material in lacking parabolae, and in having fewer primary and secondary ribs. '*Taraisites*' *carillense* Cantu Chapa (Fig. 112) and '*Rogersites*' *paucicostatus* Imlay (Fig. 113) merely seem to be based upon different growth stages of Böse's (1923) species.

Occurrence

Olcostephanus durangensis is known with certainty only from Mexico, though it may also be present in South Africa.

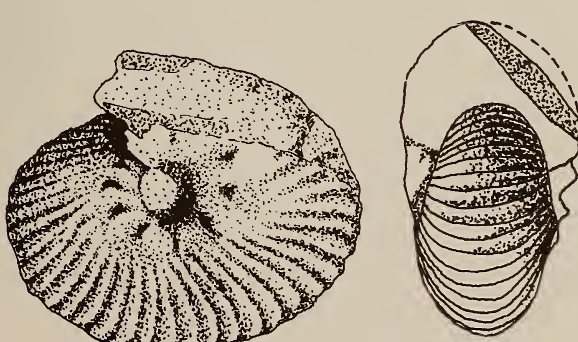

Fig. 111. *Olcostephanus* (*Olcostephanus*) *bangei* (Böse). The holotype, by monotypy, from the Taraises Formation of northern Mexico (after Böse 1923). × 1.

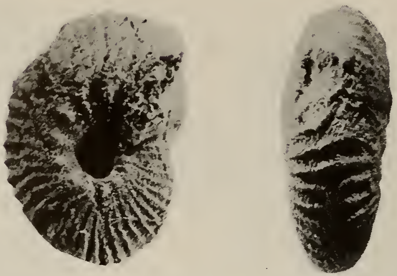

Fig. 112. *Olcostephanus* (*Olcostephanus*) *bangei* (Böse). The holotype of *Taraisites carillensis* Cantu Chapa from the Taraises Formation of northern Mexico (after Imlay 1937). × 1.

Fig. 113. *Olcostephanus* (*Olcostephanus*) *bangei* (Böse) (♀). The holotype of *Rogersites paucicostatus* Imlay from the Taraises Formation of northern Mexico (after Imlay 1937). × 1.

Olcostephanus (*Olcostephanus*) *baini baini* (Sharpe, 1856)

Figs 114–129, 130A–B, 131C–J, 132–136, 143A–B, 144A–D, 148, 150C–D, 151B–D

Microconch (♂)

Ammonites baini Sharpe, 1856: 197, pl. 23 (fig. 2a–b).
Astieria baini (Sharpe) Kilian, 1902: 866.
Holcostephanus baini (Sharpe) Kitchin, 1908: 187.
? *non Astieria* aff. *baini* (Sharpe) Böse, 1923: 76, pl. 2 (figs 3–5) (= ? *O. atherstoni*).
Rogersites baini (Sharpe) Spath, 1930: 146.
Taraisites baini (Sharpe) Cantu Chapa, 1966: 16.
Olcostephanus baini (Sharpe) Neumayr & Uhlig, 1881: 156; Riccardi *et al.*, 1971: 100.
Olcostephanus (*Rogersites*) *schenki* (Oppel) Fatmi, 1977: 270, pl. 5 (fig. 1).

Macroconch (♀)

Ammonites schenki Oppel, 1863: 286, pl. 81 (fig. 4a–c).
Astieria schenki (Oppel) Pavlow (*in* Pavlow & Lamplugh), 1892: 493.
Holcostephanus (*Astieria*) *schenki* (Oppel) Uhlig, 1903: 130, pl. 18 (fig. 2a–c only).
Astieria atherstoni (Sharpe) Baumberger, 1907: 39, figs 115–116 only.
Holcostephanus schenki (Oppel) Kitchin, 1908: 193, 198, 202–204. Kilian, 1910: 177. Spath, 1930: 150. Besairie, 1930: 629, pl. 64 (fig. 1–1a).
Holcostephanus cf. *atherstoni* (Sharpe) Kitchin, 1908: 193.
Rogersites douvillei Besairie, 1932: 44, pl. 5 (fig. 9–9a), fig. 2; 1936: 138, fig. 9 no. 2.
Rogersites baini var. *ambikyi* Besairie, 1936: 138, pl. 13 (fig. 5), fig. 9 no. 3.
Olcostephanus (*Rogersites*) *schenki* (Oppel) Spath, 1939: 30, pl. 2 (? fig. 6), pl. 18 (figs 9–10).
? *Olcostephanus sublaevis* Spath, 1939: 21, pl. 3 (figs 1–3), pl. 19 (fig. 2).
Holcostephanus douvillei (Besairie) Collignon, 1962: 43, fig. 869.
Olcostephanus atherstoni (Sharpe) Riccardi *et al.*, 1971, pl. 13 (fig. 5a–c only).
Olcostephanus schenki (Oppel) Riccardi *et al.*, 1971: 91, 97.

Material

42 specimens; 16 microconchs (PEM–1463/40a, b, 1462/76, SAM–PCU1528, 1530, 1535, 1540, 1548, AM–429c, BM–C52052, AAS–369a, SAM–525, 581, 583), 23 macroconchs (SAM–316, 1579, 5072, 6157, LJE–989d, PEM–1463/41, 1468/79, 1468/89, SAM–PCU1533, 1538, 1546, 1565, 1570, 1591, 1600, 1602, 1609, AAS–369b, 370, BM–C47122, AM–2345, 2346), and 3 juveniles (SAM–PCU1536, 1579, LJE–989f).

Holotype

By monotypy, the original of *Ammonites baini* figured by Sharpe (1856: 197, pl. 23 (fig. 2a–b)) (Fig. 114) from the Sundays River.

Diagnosis

Dimorphic. Microconch small (about 50 mm diameter), rather inflated. Primary ribs rursiradiate, terminating in 14–18 sharp umbilical bullae, from which arise 2–3 coarse, prorsiradiate secondaries, often with an intercalated rib between bundles. Usually two prominent parabolae per whorl. Peristome with lateral lappets. Macroconch very large (about 250 mm diameter), very strongly inflated, with a greatly depressed whorl section. Primary ribs rursi-

Fig. 114. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe) (♂). The holotype, in the British Museum (Natural History). × 1. Photo: W. J. Kennedy.

radiate, terminating in 17–22 bullae on the body chamber, from which arise bundles of 3–5 prorsiradiate secondaries, with 1–2 intercalatories between bundles. Parabolae present on inner whorls only. Inflation decreases on adoral portion of the body chamber.

Description

Microconch (♂): the shell is small, rarely larger than 60 mm diameter, and involute up to the umbilical bullae on the inner whorls, so that about 80 per cent of the preceding whorl is covered, but becoming slightly more evolute as the umbilical seam egresses on the adoral portion of the body chamber. Consequently, a short distance of the secondary ribbing of the penultimate whorl is visible below the umbilical seam at this stage. The whorls are rather inflated, with a depressed whorl section, the latter tending to become coronate as the umbilical seam egresses. Prominent primary ribs begin at the umbilical seam and curve backwards (rursiradiate) to distinct, sharp umbilical bullae on the umbilical shoulder. Each bulla gives rise to two or three coarse, prorsiradiate secondaries, frequently with an intercalated rib between bundles. Where there are three secondaries per bundle the intercalated rib is usually absent. Often a rib which is seen to arise from a bulla on the one flank is found to be intercalated on the other side. The secondaries recurve slightly so as to cross the venter transversely. In some specimens there may be a slight concave inflexion of the secondaries along the siphonal line. There are 14–18 bullae on the final whorl, with 17–18 secondaries per 6 bullae. The umbilicus is rather narrow and moderately deep, with steep umbilical walls and a subrounded shoulder. The slope of the umbilical wall lessens as the umbilical seam egresses. There are usually two deep parabolae per whorl, commonly about 180° apart. As is characteristic of parabolae, they truncate the ribbing adapically, and are parallel to the adoral ribs. The peristome is virtually identical to these para-

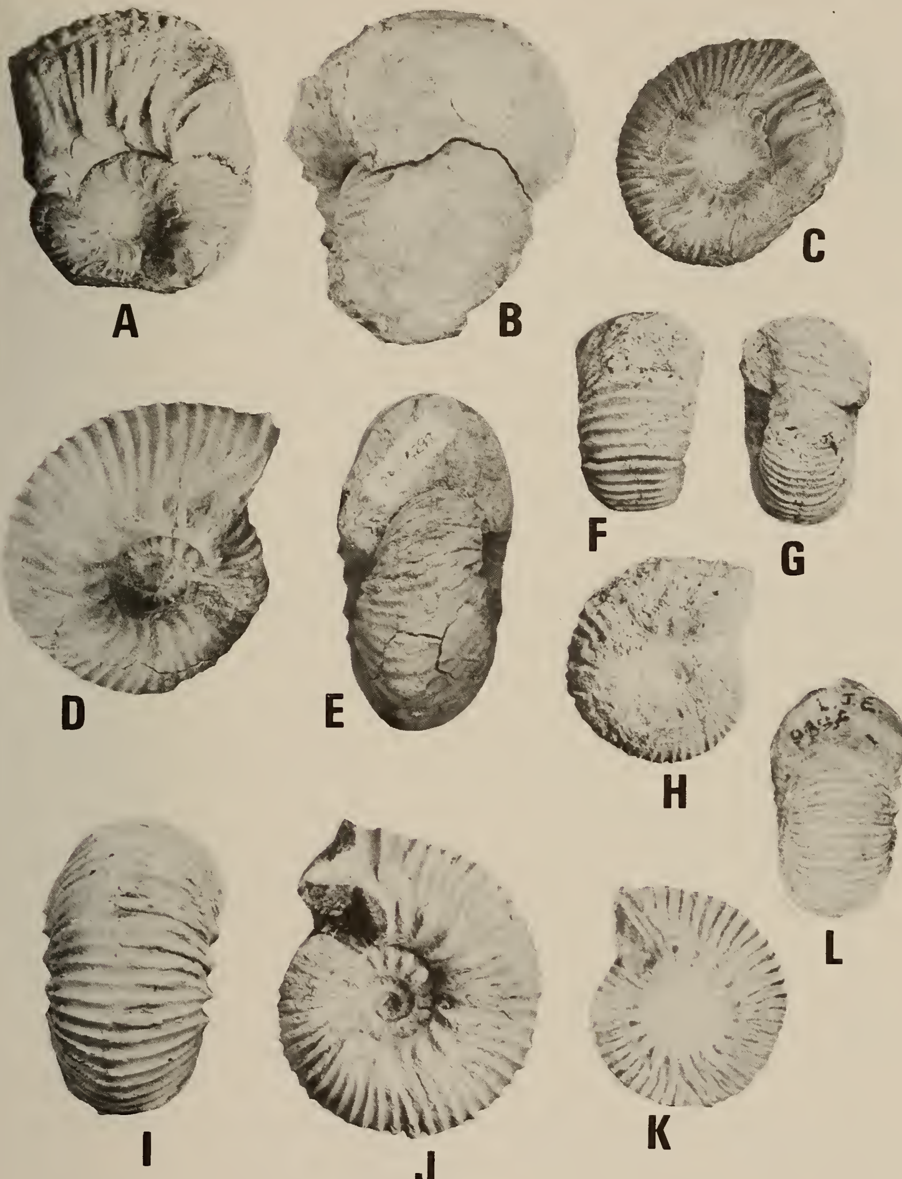

Fig. 115. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe). A–C. Lateral, front and lateral views of the inner whorls of AM–2346, an immature macroconch, × 075. D–E. Lateral and front views of AM–4292*c*, a microconch, × 0,75. F–H. Ventral, front and lateral views of a juvenile, SAM–PCU1536, doubtfully included here. Note the flattened venter and quadrate whorl section, × 1. I–J. Ventral and lateral views of a microconch in the Albany Museum, × 1. K–L. Lateral and front views of LJE–989f, × 0,75.

Fig. 116. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe) (♂). Reconstruction of the peristome of the microconch. × 1.

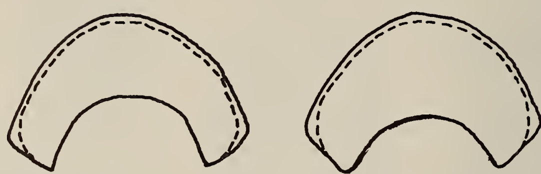

Fig. 117. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe) (♂). Whorl sections of SAM–PCU1528 (left), PEM–1462/76 (right). × 1.

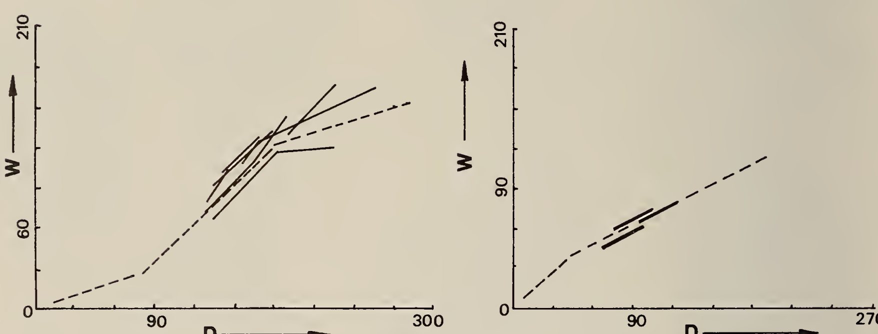

Fig. 118. Plot showing the differing rates of inflation for macroconchs of *O. baini* (left) and *O. atherstoni* (right). Note increased rate of inflation in middle whorls of *O. baini*.

bolae but, when preserved, the adoral margin is seen to bear slightly converging lateral lappets. The whorl section varies somewhat, from almost semicircular to coronate, with a well-rounded venter. The suture line is unknown. As in other olcostephanids the body chamber is almost a full whorl in length.

Macroconch (♀): The shell is very large, commonly around 250 mm diameter, and extremely inflated, with a strongly depressed whorl section. The earliest whorls are only moderately inflated and up to a diameter of about 60 mm closely resemble the microconch, from which they differ only in being slightly more inflated and in having invariably three secondaries per bulla,

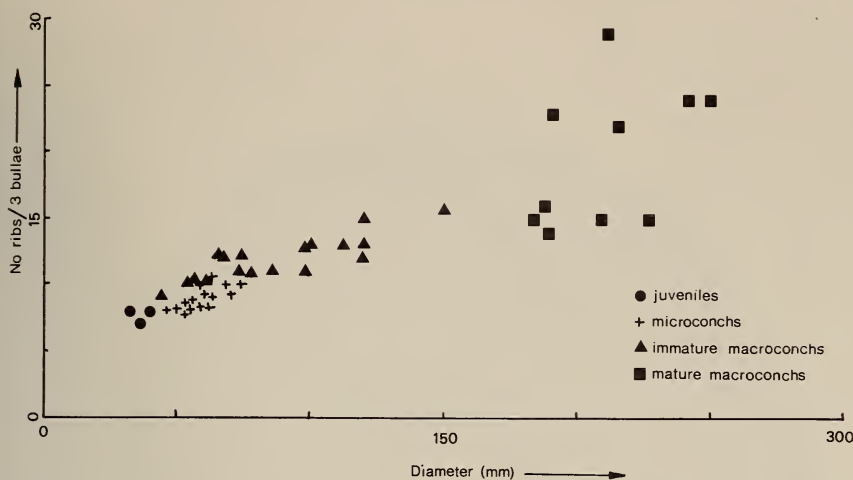

Fig. 119. Plot showing increase in rib density with ontogeny, and between dimorphs, in *O. b. baini* (Sharpe).

commonly with an intercalated rib between bundles. At this stage, the macroconch is, therefore, slightly more densely ribbed than the microconch. After about 60 mm diameter the whorl section rapidly becomes extremely inflated, reaching a maximum about one-third of a whorl behind the peristome. The umbilicus is very narrow and deep, with a vertical umbilical wall and acute shoulder. The slope of the umbilical wall becomes less steep with the egression of the umbilical seam while the umbilical shoulder also becomes distinctly rounded at this growth stage. Prominent primary ribs begin at the umbilical seam and curve backwards (rursiradiate) to terminate in 19–22 bullae on the final whorl. One specimen, SAM–PCU1591, has only 14 bullae on the outer whorl, which become extremely swollen and large near the peristome, and is with reservations referred to this species. Each bulla gives rise to bundles of usually 3–4 coarse prorsiradiate secondaries, rarely 5, with 1–2 intercalated ribs between bundles. There are between 23 and 28 secondaries per 5 bullae on the adoral portion of the body chamber, with generally fewer at earlier growth stages. The secondary ribbing is slightly flexuous, recurving on the flanks so as to cross the venter transversely. At 155 mm diameter (PEM–1468/79) there are 24 secondaries per 6 bullae, and 9 ribs within a 50 mm distance along the venter. In the same specimen at 210 mm diameter there are 21 secondaries per 4 bullae, with a rib spacing of 7 mm. The inner whorls of macroconch dimorphs of *O. baini* have prominent, deep parabolae, the largest diameter at which they are seen to occur being 130 mm. However, in some examples taken to belong to this dimorph by virtue of their very strong inflation, there is no sign of parabolae at smaller diameters. This would seem to suggest that the growth stage at which parabolae ceased to be produced varies from individual to individual, although it would generally seem to be at about 90–120 mm

Fig. 120. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe) (♀). Front and lateral views of SAM–5072. Note homoeomorphic resemblance to *O. atherstoni*. × 0,44.

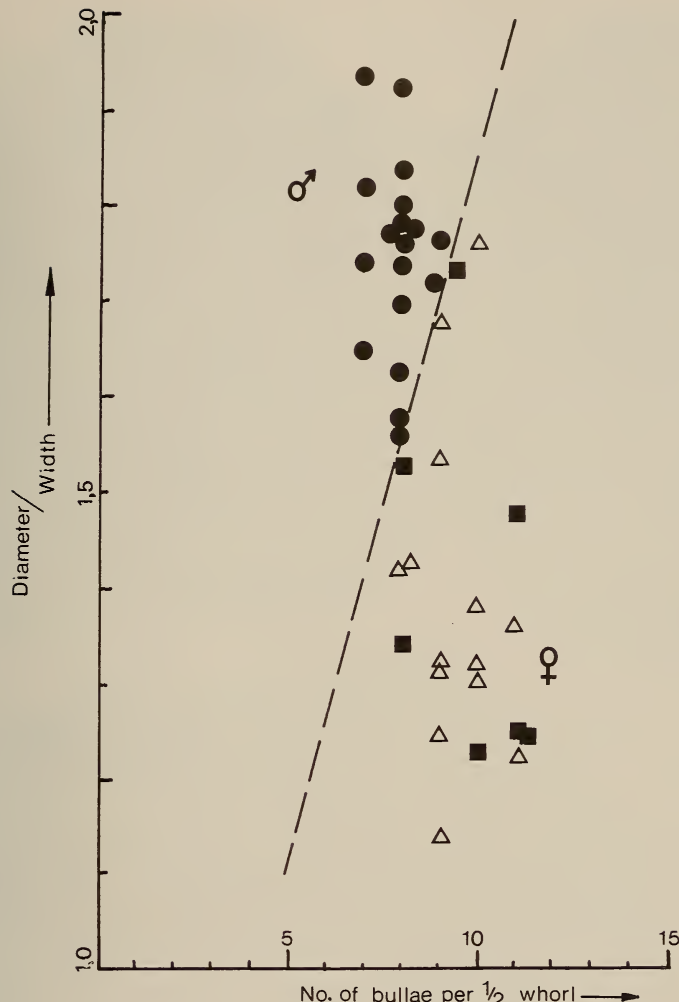

Fig. 121. Plot showing the relationship between inflation (Diameter/Width) and number of umbilical bullae per half whorl in *O. b. baini* dimorphs. Dots = microconchs, triangles = immature macroconchs, squares = mature macroconchs.

diameter. Parabolae never occur on the outer whorls of macroconch forms, although the peristome takes the form of a parabola.

Measurements

No.	D	H	Wi	W/H	Uo	Ui
AM–2344	50	21	31	1,48	17	9 (18)
AM–2345	68	26	46	1,77	25	13 (19) (♀)
,,	56	22	32	1,45	18	10 (18)

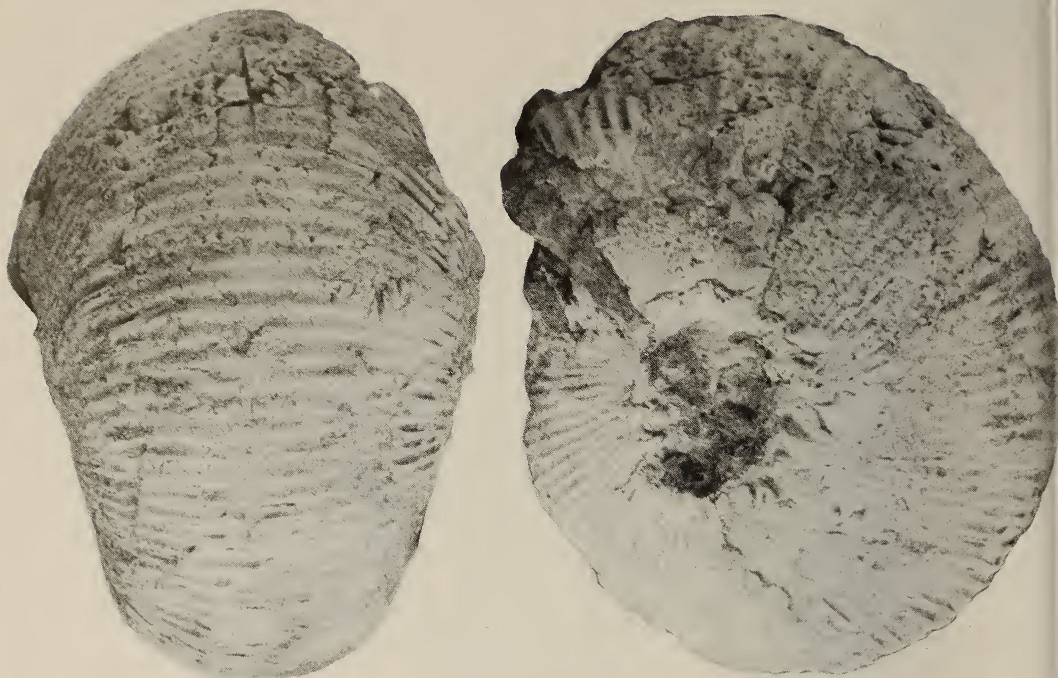

Fig. 122. *Olcostephanus* (*Olcostephanus*) cf. *baini* (Sharpe) (♀). Ventral and lateral views of a specimen in the British Museum (Natural History). × 0,66.

No.	D	H	Wi	W/H	Uo	Ui
PEM–1468/73	180	82	135	1,65	70	44 (24) (♀)
,,	135	62	90	1,45	50	27 (20)
SAM–PCU1591	255	115	166	1,44	90	52 (20) (♀)
,,	174	85	150	1,76	69	?
PEM–1468/89	250	92	155	1,68	110	82 (33) (♀)
,,	167	83	126	1,52	65	43 (26)
PEM–1468/79	225	87	122	1,40	83	46 (20) (♀)
,,	184	79	120	1,52	56	31 (17)
SAM–316	208	93	138	1,48	78	47 (22) (♀)
,,	145	60	100	1,67	55	?
PEM–1468/80	170	100	?		?	? (♀)
,,	140	75	?		?	?
AM–2346	55	23	37	1,61	27	17 (31) (♀)
,,	38	13	21	1,61	13	7 (18)
,,	24	11	17	1,55	10	4 (17)
SAM–PCU1546	226	108	170	1,57	55	43 (19) (♀)
,,	190	85	132	1,55	?	?

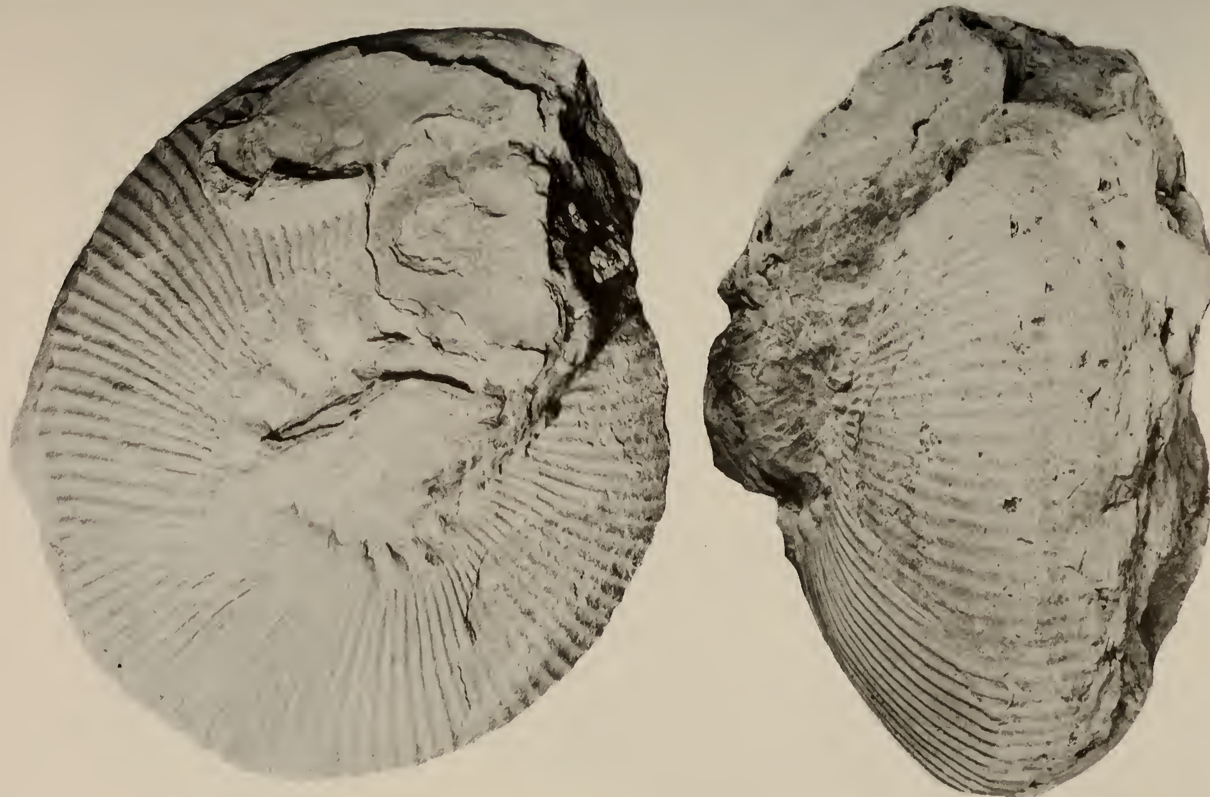

Fig. 123. *Olcostephanus* (*Olcostephanus*) *baini* (Sharpe) (♀). Lateral and front views of SAM–PCU1546. Note encrusting oysters, one of which fills the umbilicus. × 0,44.

Fig. 124. *Olcostephanus* (*Olcostephanus*) *baini* (Sharpe) (♀). Front and lateral views of PEM–1468/79, showing maximum inflation about one-third of a whorl behind the peristome. × 0,44.

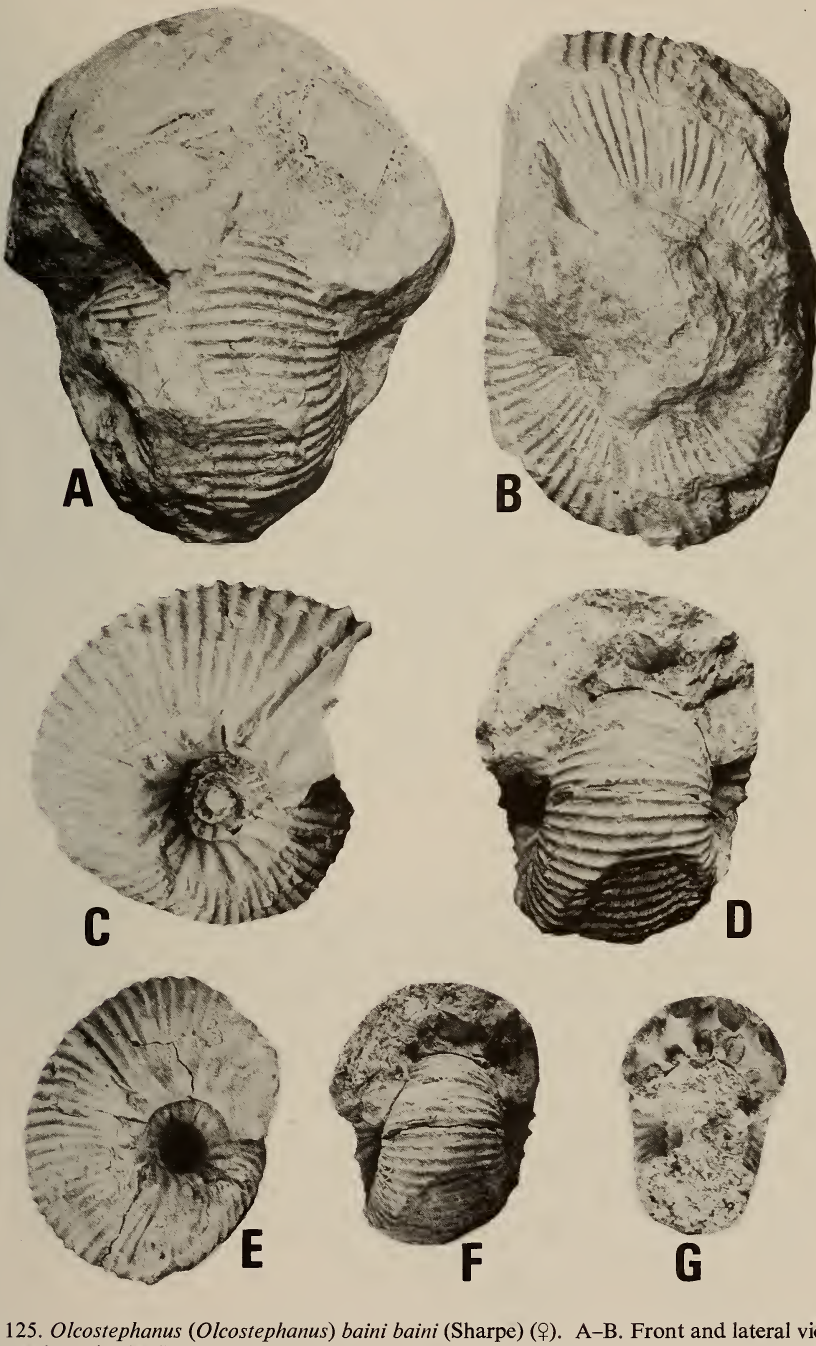

Fig. 125. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe) (♀). A–B. Front and lateral views of a specimen in the South African Museum, × 0,44. C–D. Lateral and front views of SAM–PCU1533, an immature macroconch, × 0,75. E–G. Lateral, front and cross-sectional views of inner whorls of SAM–PCU1533, × 0,75.

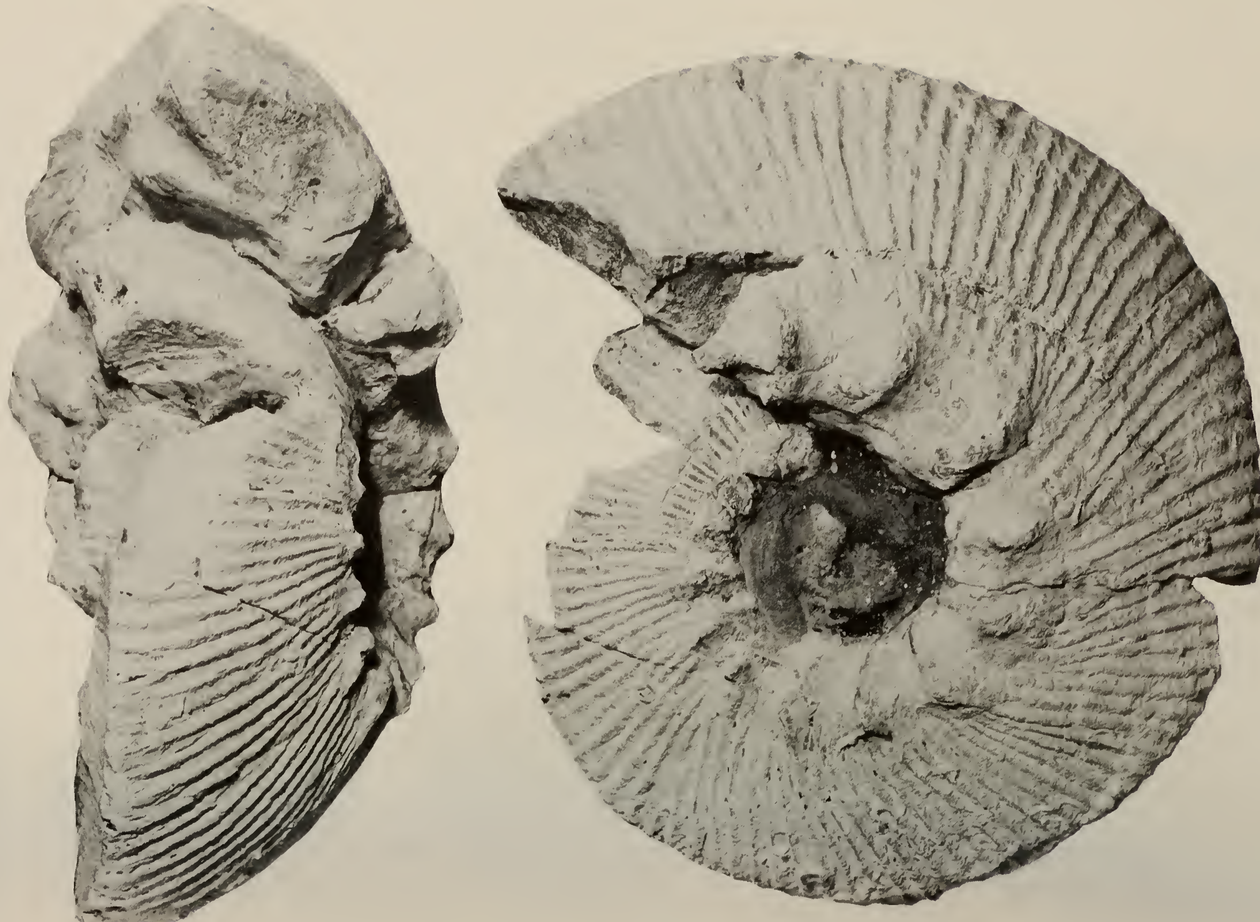

Fig. 126. *Olcostephanus* (*Olcostephanus*) cf. *baini baini* (Sharpe) (♀). Front and lateral views of SAM–PCU1591. Note the swollen umbilical bullae. × 0,44.

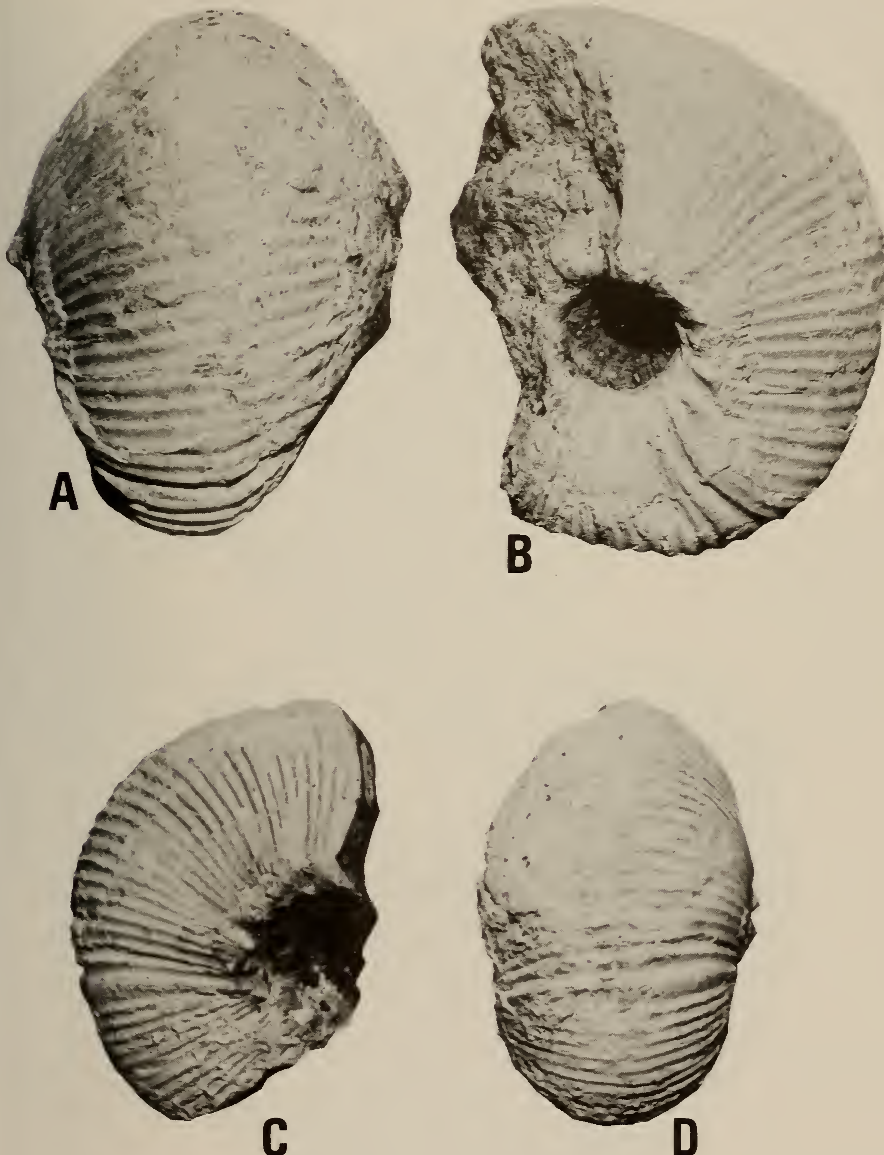

Fig. 127. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe) (♀), × 0,44. A–B. Ventral and lateral views of SAM–PCU1609. C–D. Lateral and ventral views of SAM–PCU1570.

Fig. 128. *Olcostephanus* (*Olcostephanus*) *baini* (Sharpe) (♀). Lateral and ventral views of a somewhat crushed specimen, PEM–1468/80. × 0,44.

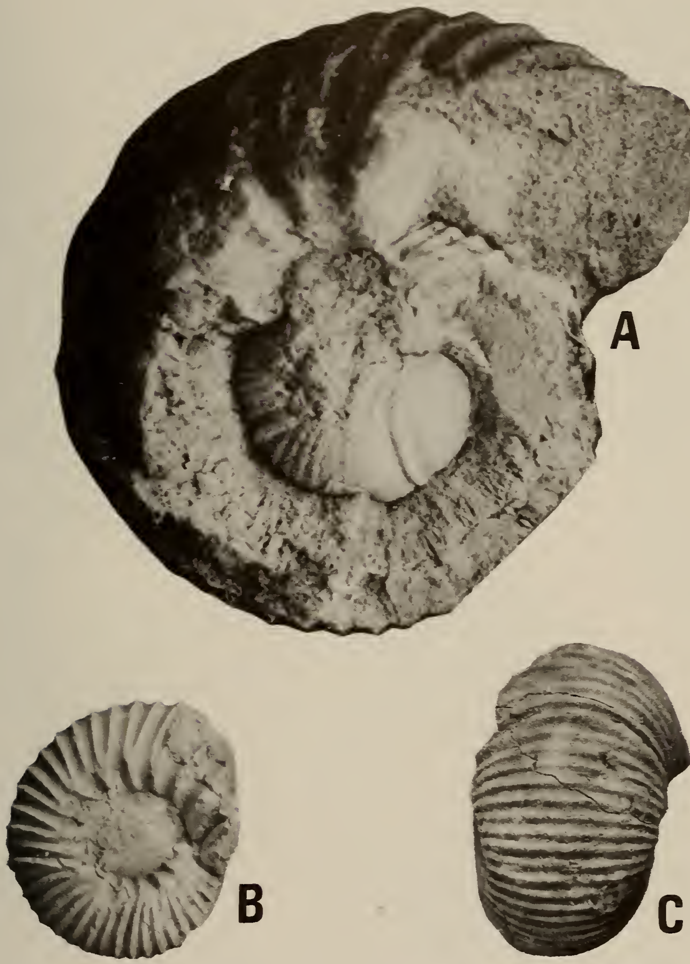

Fig. 129. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe). A. A nucleus which possibly belongs here, in the South African Museum. Note the prominent parabolae at a stage when ribs are still absent, × 2,5. B. Lateral view of a microconch, BM–52052, × 1. C. Ventral view of an immature macroconch, SAM–PCU1533, × 1.

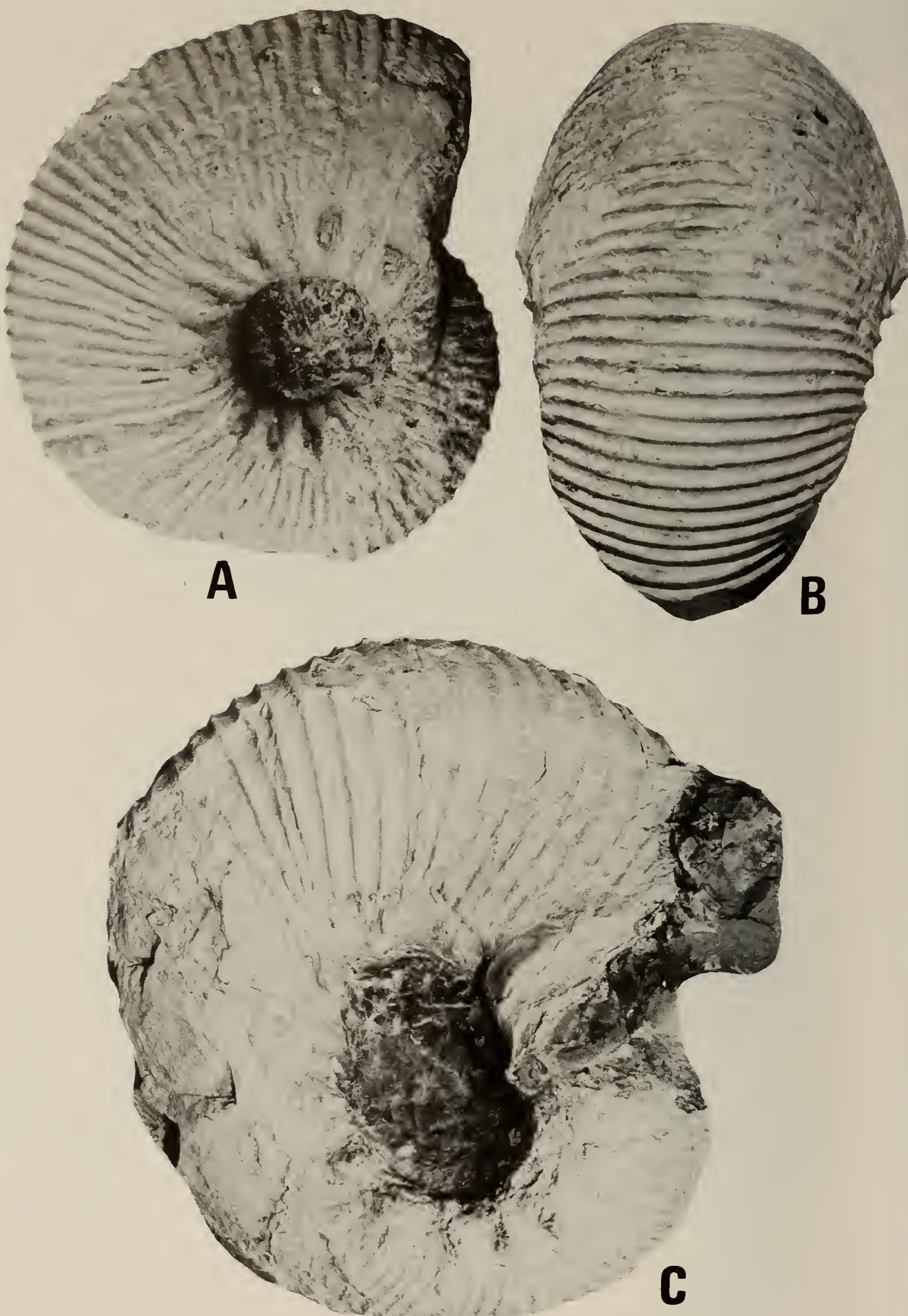

Fig. 130. A–B. *Olcostephanus* (*Olcostephanus*) cf. *baini* (Sharpe) (♀). Lateral and ventral views of AAS–369b, somewhat resembling *O. actinotus* (Baumberger), but with parabolae. × 0,75. C. *Olcostephanus* (*Olcostephanus*) sp. (♀). Lateral view of a crushed macroconch, SAM–PCU1551. Note peristome and coarse ribbing on adoral portion of the body chamber. × 0,44

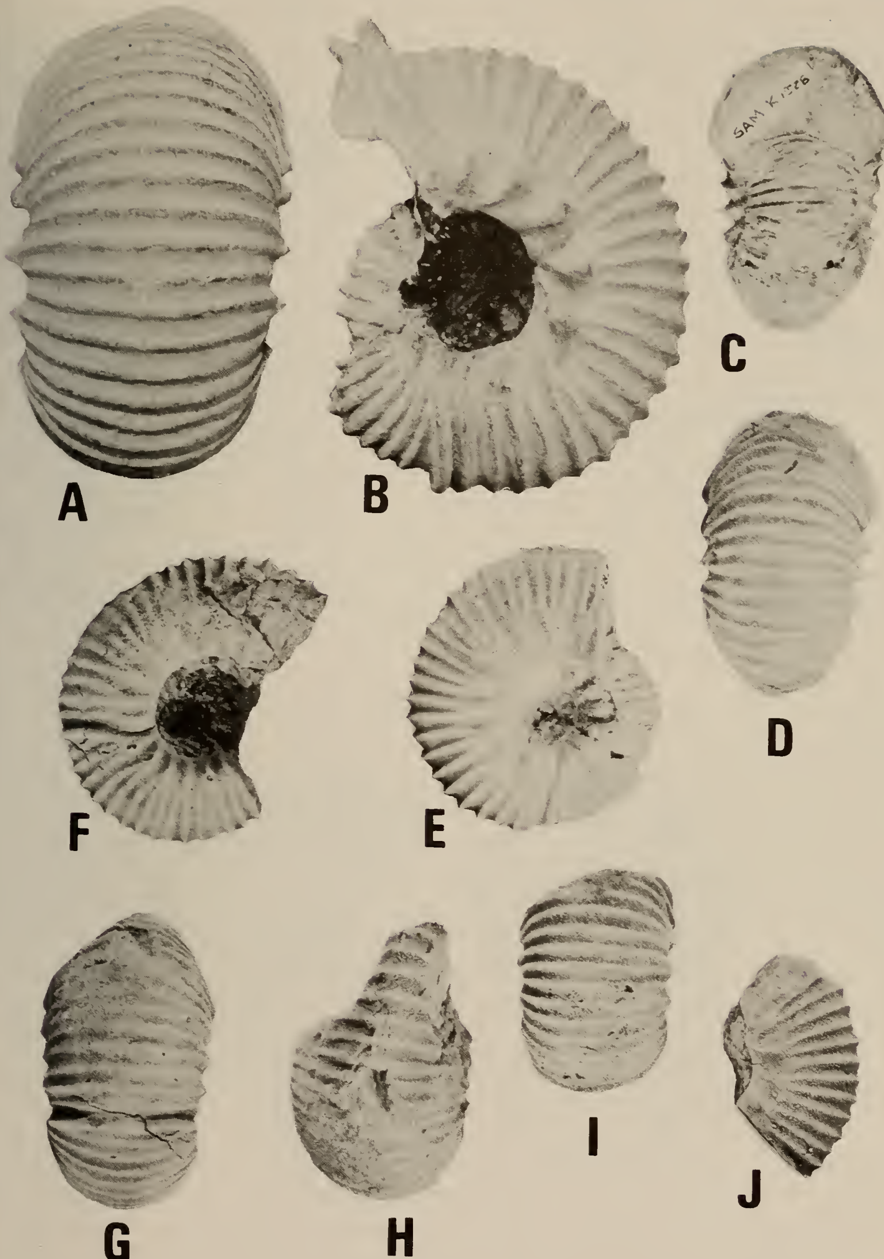

Fig. 131. A–B. *Olcostephanus* (*Olcostephanus*) cf. *rogersi* (Kitchin) (♂). Ventral and lateral views of SAM–PCU1527. Note inflexion in the apertural constriction which is lacking in the parabola, × 0,75. C–J. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe) (♂). C–E. Front, ventral and lateral views of SAM–PCU1528. F–H. Lateral and two ventral views of PEM–1463/40a; note peculiar chevron-shaped crushing of peristomal region suggestive of a bite-mark. × 0,75. I–J. Ventral and lateral views of SAM–525, × 1.

No.	D	H	Wi	W/H	Uo	Ui
SAM–PCU1544	105	50	81	1,62	20	? (♀)
SAM–PCU1538	120	50	85	1,70	42	? (♀)
,,	87	40	57	1,42	30	?
SAM–PCU1594	150	70	115	1,64	40	28 (19) (♀)
,,	130	52	80	1,54	43	27 (21)
AM–2978	50	15	27	1,80	23	12 (24) (♂)
,,	40	16	22	1,38	17	7 (18)
PEM–1463/40a	39	17	22	1,29	21	11 (28) (♂)
,,	28	9	16	1,78	?	?
LJE–989f	27	7	14	2,00	11	6 (22) (♂)
,,	17	5	10	2,00	8	3 (18)
AAS–369a	43	15	21	1,40	20	10 (23) (♂)
,,	30	9	16	1,78	?	?
PEM–1462/76	48	15	24	1,60	21	12 (25) (♂)
,,	30	11	20	1,82	13	7 (23)
SAM–PCU1528	50	17	24	1,41	22	12 (24) (♂)
,,	38	12	18	1,50	15	7 (18)
PEM–1468/76	65	22	33	1,50	25	13 (20) (♂)
,,	51	17	22	1,29	18	9 (18)

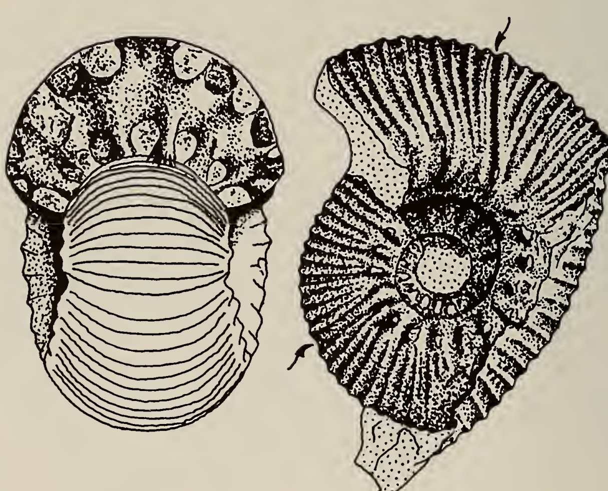

Fig. 132. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe) (♀). The holotype of *Olcostephanus schenki* (Oppel) from the Salt Range of Pakistan (after Uhlig 1903). × 1.

Fig. 133. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe) (♀). The holotype of *Rogersites douvillei* Besairie (*fide* Collignon 1962) and also *Rogersites baini* var. *ambikyi* Besairie, from the Upper Valanginian of Ambiky, Madagascar (after Collignon 1962). × 1.

Discussion

As has been pointed out by many previous workers, *O. baini* (♂) forma typica bears a close resemblance to *O. schenki* (Oppel) (Fig. 132). It becomes apparent from the present study that the differences are merely those due to a comparison of the inner whorls of a macroconch with a microconch form. Consequently, *O. schenki* (Oppel) is regarded as a junior subjective synonym of *O. baini baini*. Riccardi *et al.* (1971) considered *O. schenki* to represent the inner whorls of the *O. atherstoni* macroconch. However, as warned by Makowski (1962*a*: 21), they failed to recognize the homoeomorphy between macroconch forms. Hence the *O. atherstoni* fauna recorded by Riccardi *et al.* (1971) from west-central Argentina includes both *O. atherstoni* and *O. b. baini*, as evidenced by the presence of young macroconchs both with and without parabolae. This same phenomenon recurs in the Uitenhage fauna, the homoeomorphy being recognized by the differing rates of inflation of the two forms (Fig. 118).

Olcostephanus douvillei (Besairie) (Fig. 133) was erected for strongly inflated forms with commonly three prorsiradiate secondaries per bulla, and parabolae on the inner whorls. This species is undoubtedly conspecific with the *O. b. baini* macroconch, representing merely an immature growth stage. *Olcostephanus baini* var. *ambikyi* Besairie has the same holotype as *O. douvillei* and is thus a junior objective synonym.

In 1930, Besairie figured an example of *O. schenki* (Oppel) which he considered '. . . tout a fait semblable aux figures d'Uhlig'. The large size and numerous secondaries, together with the presence of parabolae, suggest this

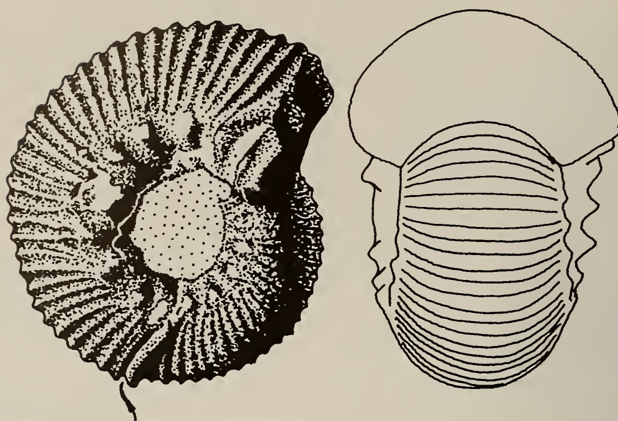

Fig. 134. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe) (♀). The specimen figured by Spath (1939) as *R. schenki* (Oppel), and considered to represent the holotype by Collignon (1962) (after Spath 1939). This is an immature macroconch. × 1.

specimen represents the inner whorls of an *O. baini* macroconch. This example does not, however, show the rapid inflation which characterizes the Uitenhage forms at a similar growth stage. Collignon (1962: 36), in refiguring Besairie's specimen, made the interesting assertion that Uhlig had, in error, figured the wrong specimen as Oppel's holotype, and that the specimen of *O. schenki* figured by Spath (1939, pl. 18 (fig. 9a–b)) (Fig. 134) was, in fact, the holotype. There appears no justification, however, in this assertion since, according to Oppel (1863: 287), the holotype came from 'Schangra, west of Puling in Gnari-Khorsum (Tibet)', whereas Spath's specimen came from '. . . near loc. 682', i.e. the northern side of Maranwal Nala, Makerwal Colliery. To suggest that Spath's specimen is the actual holotype would suggest that both Uhlig (1903) and Spath (1939) had made the same mistake (A. C. Riccardi pointed out this fact to the author).

Olcostephanus sphaeroidalis (Spath) is a macroconch form erected for those species differing from *O. atherstoni* (♀) in their greater inflation and more depressed whorl section. These are the characters which distinguish the *O. baini* macroconch from that of *O. atherstoni*. It is of interest to note, therefore, that a re-examination of Spath's holotype shows the inner whorls to bear parabolae. Since the outer whorls of the macroconchs of *O. baini* (Sharpe) and *O. sphaeroidalis* (Spath) cannot be distinguished, the latter is treated as a variety of the former.

Olcostephanus (*Subastieria*) *nicklesi* Wiedmann & Dieni (Fig. 48) closely resembles the microconch of *O. baini baini*, from which it differs largely in having a sloping umbilical wall at all growth stages. This causes the umbilical bullae to be situated at about mid-flank, resulting in a pentagonal whorl section. This subtle difference is readily apparent, but whether it is of subgeneric rank

Fig. 135. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe) (♀). The holotype of *Rogersites tsimihetensis* Besairie from the Upper Valanginian of Ambiky, Madagascar. Parabola arrowed. × 1.

would seem to depend on the recognition of sexual dimorphism in this subgenus, if it exists, and the morphology of the corresponding macroconch. It is of interest to note that Wiedmann & Dieni (1968) included forms both with and without parabolae in their species.

In 1923 Böse recorded a specimen of '*Astieria* aff. *baini*' from the Taraises Formation of northern Mexico. Cantu Chapa (1966) subsequently made this specimen the type of his new genus *Taraisites*, renaming it *T. bosei* (Fig. 9). This genus was erected within the new subfamily Taraisitinae for those forms of *Olcostephanus* in which 2–3 secondaries arise from each umbilical bulla. Riccardi *et al.* (1971) have already shown this genus to be a synonym of *Olcostephanus* s.s., also supported by the fact that the *Ammonites baini* of Sharpe, assigned to *Taraisites* by Cantu Chapa (1966), represents nothing more than the microconch of a much larger, more densely ribbed macroconch. The preservation of '*Taraisites bosei*' leaves much to be desired, but as it appears to lack parabolae, and in view of the abundance of *O. atherstoni* in these beds, it is probably best referred to that species.

The holotype of '*Rogersites*' *tsimihetensis* Besairie (Fig. 135) is poorly preserved but shows no features whereby it can be distinguished from the *O. baini* macroconch. It is, therefore, a junior subjective synonym of Sharpe's (1856) species.

Fig. 136. *Olcostephanus* (*Olcostephanus*) *baini* (Sharpe) (♀). The holotype of *Rogersites sanlazarensis* Imlay from the Taraises Formation of northern Mexico (after Imlay 1937). × 1.

'*Rogersites*' *sanlazarensis* Imlay (Fig. 136) was created for large, fairly inflated forms with a deep and narrow umbilicus, and steep umbilical walls. About 18 rursiradiate primaries terminate in small umbilical bullae from which arise bundles of 3–4 prorsiradiate secondaries, with 1–2 intercalated ribs between bundles. The inner whorls bear prominent parabolae. It is clear from the above description and figure that '*R.*' *sanlazarensis* should be considered a junior subjective synonym of the *O. baini* macroconch, perhaps of the variety *sphaeroidalis* (Spath).

'*Astieria*' *taurica* Karakasch (Fig. 137) resembles the *O. baini* microconch, but has more numerous constrictions and seems to lack umbilical bullae to most secondary ribs. This species is very close to *Jeanthieuloyites quinquestriatus* (Besairie), from which it seems to differ in that the secondary ribs do not bifurcate before crossing the venter. It is, however, perhaps best referred to this genus.

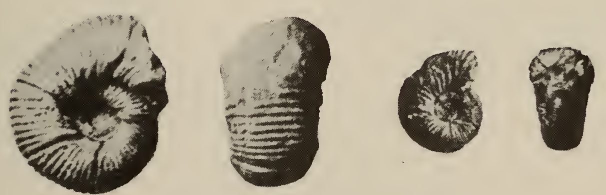

Fig. 137. *Olcostephanus* (?*Subastieria*) *tauricus* (Karakasch). The syntypes, of which the larger is herein selected as lectotype, from Crimea (after Karakasch 1907). × 1.

Fig. 138. *Olcostephanus* (?*Subastieria*) *pavlowi* (Karakasch). The holotype, by monotypy, from the Upper Valanginian of the Crimea (after Karakasch 1907). × 1.

'*Astieria*' *pavlowi* Karakasch (Fig. 138) is based upon a tiny individual with a strongly depressed whorl section, narrow umbilicus, rursiradiate secondaries and prominent parabolae. It was compared with *O.* (*Subastieria*) *sulcosus* Pavlow (*in* Pavlow & Lamplugh 1892) and differs from *O. baini* in the rursiradiate direction of its secondary ribbing.

Olcostephanus hispanicus (Mallada 1882) was considered to lie at the 'triple-junction' of the subgenera *Parastieria*, *Subastieria* and *Olcostephanus* by Wiedmann & Dieni (1968), although they placed the holotype within the subgenus *Subastieria*. The writer has not seen Mallada's (1882) original figure or description but, as figured by Nicklès (1890), this species is remarkably similar

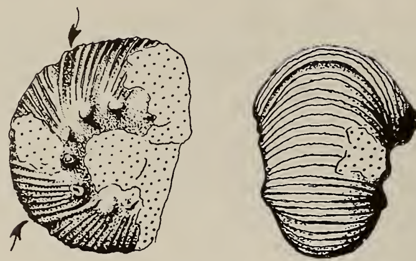

Fig. 139. *Olcostephanus* (*Olcostephanus*) *dacquei* (Krenkel). The holotype, by monotopy, from the Mikadi region of Tanzania (after Krenkel 1910). × 1.

to the inner whorls of the *O. baini* macroconch. Topotype material is necessary to determine the specific and subgeneric status of the Spanish species.

Olcostephanus dacquei (Krenkel) (Fig. 139) is based upon a juvenile with a rather narrow umbilicus and a depressed, coronate whorl section. Prominent primary ribs terminate in 7 well-developed, somewhat rounded umbilical tubercles from which arise 4–5 prorsiradiate secondaries, frequently with an intercalated rib between bundles. There are about 37 ribs per half whorl, as well as two prominent parabolae. This species differs from *O. baini* in possessing fewer umbilical tubercles from which arise finer, more numerous secondary ribs.

The holotype of *O. sublaevis* Spath (Fig. 140) is entirely septate and seems to be based upon the inner whorls of a macroconch. Based upon Fatmi's (1977) interpretation of this species, there are about 20 rursiradiate primaries (certainly more in Spath's holotype) which terminate in bullae on the umbilical shoulder and give rise to 4–6 slightly flexuous, prorsiradiate ribs. There is little to distinguish this species from the *O. baini* macroconch, of which it seems

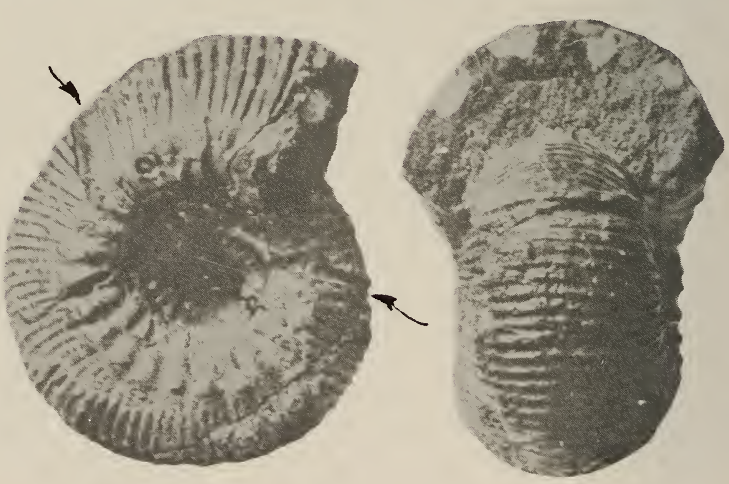

Fig. 140. *Olcostephanus* (*Olcostephanus*) *sublaevis* Spath (♀). The holotype from the Spiti Shales of Pakistan (after Spath 1939). × 1.

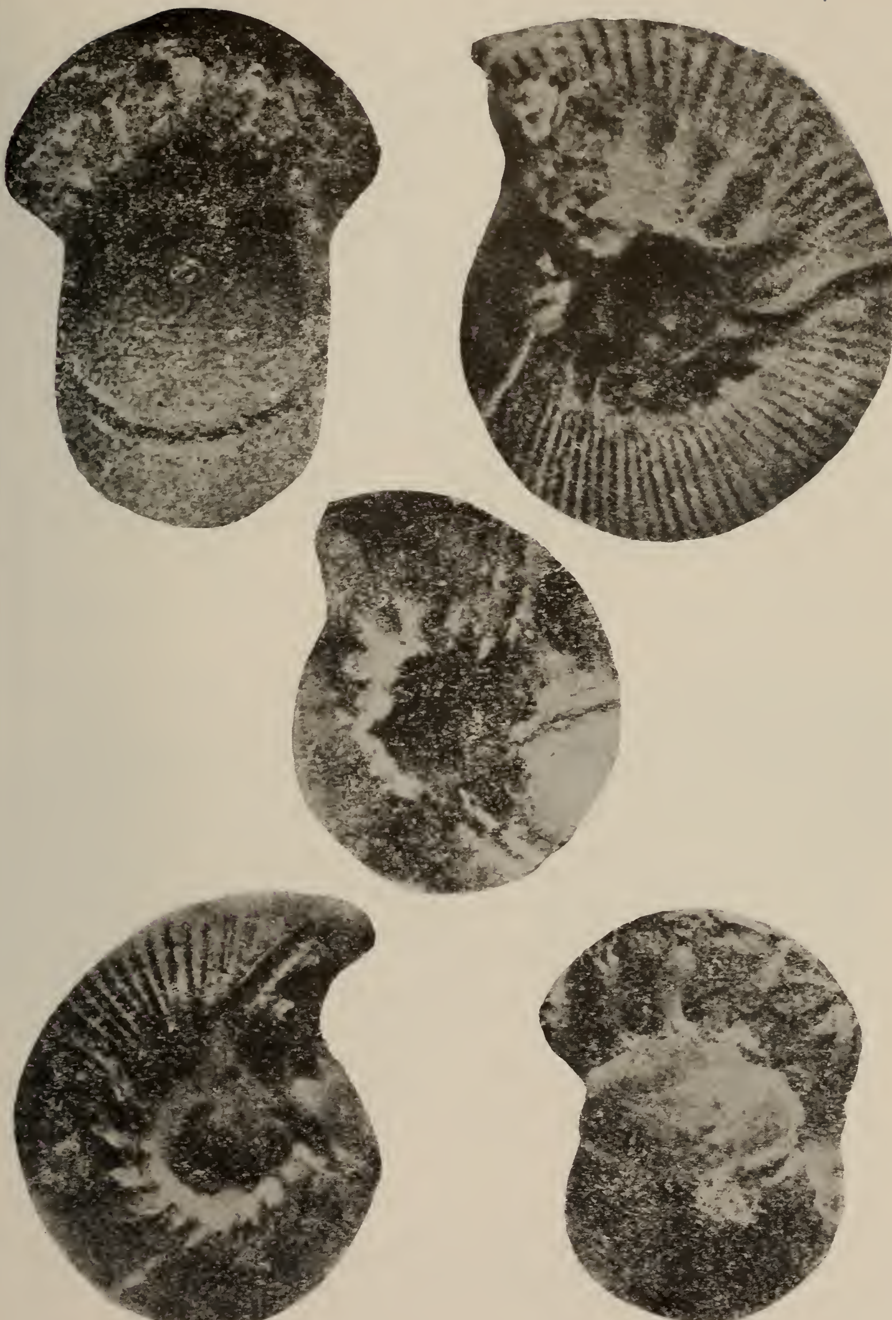

Fig. 141. *Olcostephanus* (*Olcostephanus*) *inordinatus* (Tzankov). The syntypes from the Upper Valanginian–Lower Hauterivian of Tchakantsi, Bulgaria, of which the upper specimen is herein selected as lectotype (after Tzankov 1943). × 5.

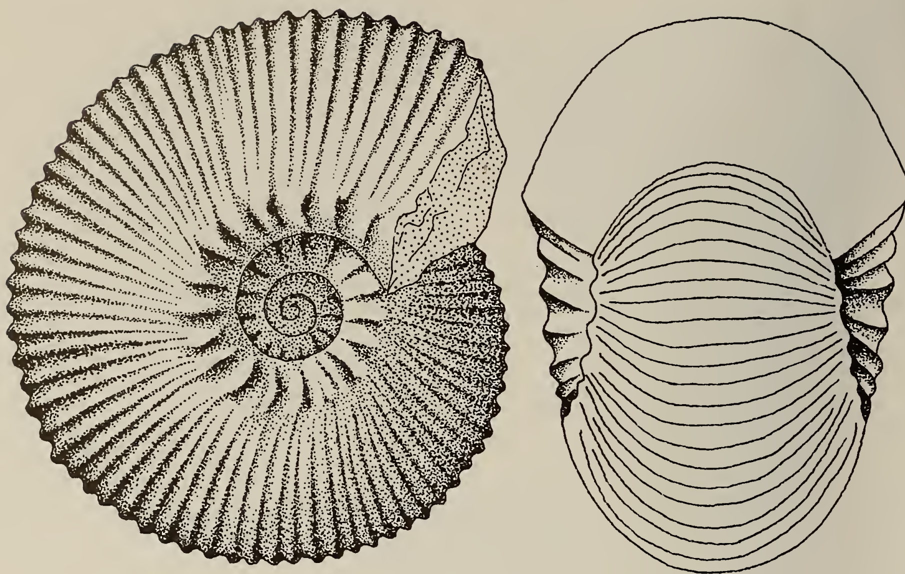

Fig. 142. *Olcostephanus* (*Olcostephanus*) *inordinatus* (Tzankov) (♀) (after Pictet 1860). × 1.

merely to represent an early growth stage. *Olcostephanus sublaevis* is tentatively included in the synonymy of *O. baini*.

Olcostephanus inordinatus (Tzankov) (Fig. 141) was based upon nuclei, some of which are still partially smooth and hence comparison is difficult. At this growth stage the whorl section is coronate, strongly depressed, and the umbilicus is fairly narrow, with sloping umbilical walls. There seem to be between 15 and 17 umbilical bullae on the outer whorl of the largest individual, which is herein selected as lectotype, from which arise 3–4 prorsiradiate secondary ribs. There are prominent parabolae. Since Tzankov (1943) included the specimen figured by Pictet (*in* Pictet & Campiche 1860, pl. 17 (fig. 4), pl. 18 (fig. 3)) (Fig. 142) into this species, this suggests that *O. inordinatus* loses its parabolae in maturity. There is, thus, little to distinguish Tzankov's (1943) species from the *O. baini* macroconch, of which it may prove to be a synonym.

As already pointed out, *O. crassicostatus* (Spath) (Fig. 80) was originally compared with *O. baini* but is herein interpreted as a gerontic *O. rogersi* (Kitchin) microconch.

Occurrence

As interpreted here, this species appears to be known from Tibet, Pakistan, ?Spain, Madagascar, Argentina, northern Mexico, ?Oregon, and South Africa, while the occurrence of strongly inflated forms with constricted inner whorls in the Swiss Jura and Bulgaria suggests its presence in these areas as well.

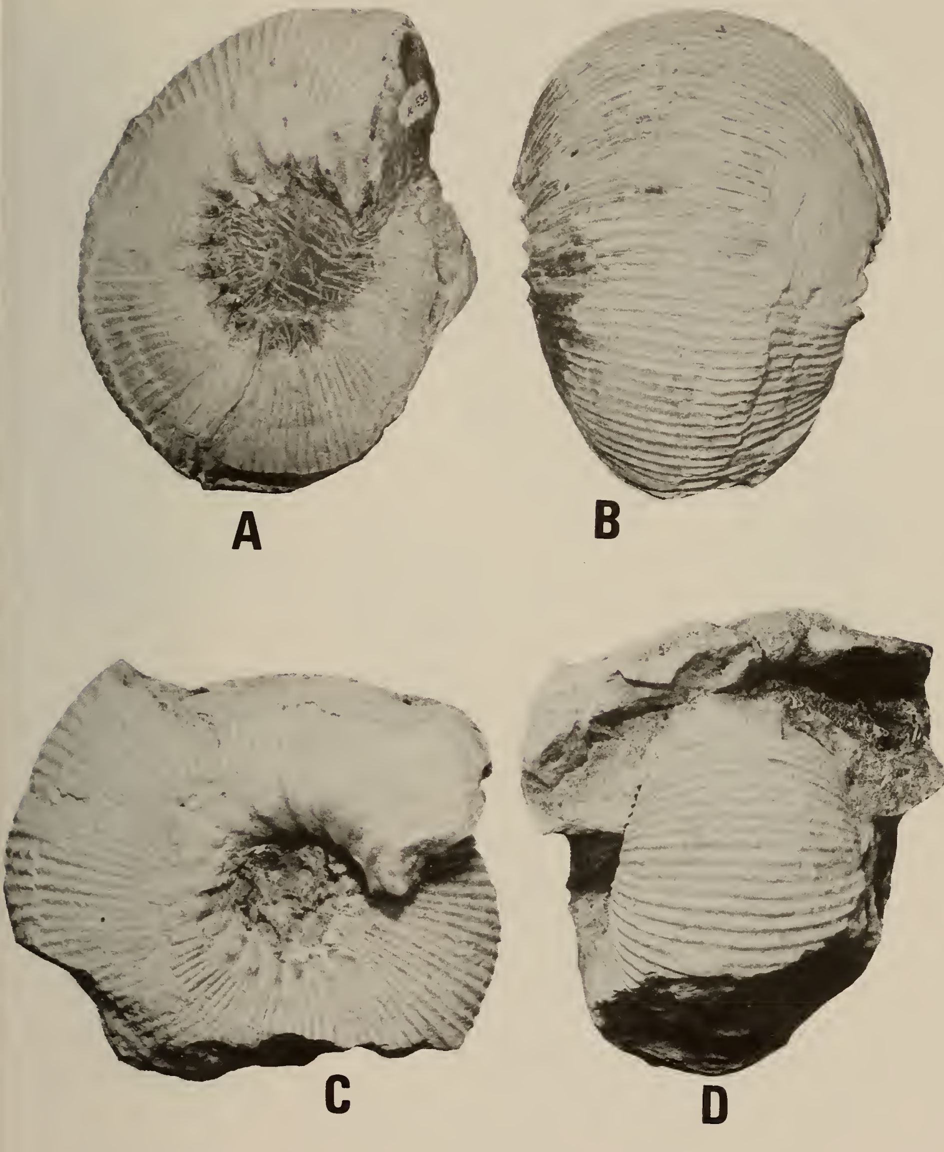

Fig. 143. A–B. *Olcostephanus* (*Olcostephanus*) *baini* (Sharpe) (♀). Lateral and ventral views of SAM–PCU1538, × 0,50. C–D. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♀) Lateral and front views of SAM–PCU1604, × 0,66.

Olcostephanus (*Olcostephanus*) *baini* var. *sphaeroidalis* (Spath, 1930)

Figs 144E–G, 145–150A–B, F, 153

Microconch (♂)

? *Astieria leptoplana* Baumberger, 1908: 9, pl. 26 (fig. 4 only).
? *Olcostephanus glaucus* Spath, 1939: 17, pl. 6 (figs 7–8 only).
Holcostephanus ankaranensis Collignon, 1962: 40, pl. 191 (fig. 870).
Olcostephanus (*Rogersites*) *madagascariensis* var. *isakhelensis* Fatmi, 1977: 272, pl. 5 (fig. 3).

Macroconch (♀)

Rogersites sphaeroidalis Spath, 1930: 144, pl. 13 (fig. 5), pl. 15 (fig. 1).
? *Olcostephanus sublaevis* Spath, 1939: 21, pl. 3 (figs 1–3), pl. 19 (fig. 2); Fatmi, 1977: 269, pl. 4 (fig. 2).
? *Rogersites sanlazarensis* Imlay, 1937: 560, pl. 72 (figs 1–3), pl. 74 (fig. 1).
Olcostephanus (*Olcostephanus*) *sakalavensis* Fatmi (*non* Besairie), 1977: 267, pl. 2 (fig. 3 only), pl. 3 (fig. 2), pl. 4 (fig. 3).

Material

8 microconchs (SAM–PCU1534, SAM–PCU1592, SAM–PCU1593, SAM–PCU1523, SAM–1525, PEM–1468/76, BM–C41733, BM–C41731), and 1 macroconch (SAM–9241).

Holotype

By monotypy, the original of *Rogersites sphaeroidalis* figured by Spath (1930: 144, pl. 13 (fig. 5), pl. 15 (fig. 1)) from the Sundays River and now in the South African Museum, SAM–9241.

Diagnosis

Microconch moderately small, about 70–80 mm diameter, rather compressed but with a depressed whorl section. Rursiradiate primaries terminate in 18–22 umbilical bullae from which arise bundles of 3–4, rarely only 2, prorsiradiate secondaries. Parabolae prominent. Macroconch large, outer whorls indistinguishable from those of *O. b. baini* Inner whorls more finely ribbed, with commonly 4 secondaries per bulla, and 1–2 intercalated ribs between bundles. Parabolae present on inner whorls.

Description

Microconch (♂): moderately small cadicones, about 70–80 mm diameter, with somewhat compressed shells. The whorl section is depressed, with an evenly arched venter. The whorls are involute up to the umbilical bullae, covering about 80 per cent of the preceding whorl, except on the adoral portion of the body chamber when the umbilical seam egresses slightly.

Primary ribs begin at, or close to, the umbilical seam and curve backwards (rursiradiate) to 18–22 prominent bullae, on the umbilical shoulder of the final whorl. Secondary ribbing commonly arises in prorsiradiate bundles of 3–4, rarely only 2, often with an intercalated rib between bundles. The secondary ribbing recurves on the flanks so as to cross the venter transversely. There may be a slight adorally concave inflexion where the ribbing crosses the siphonal line. Along the venter of the adoral portion of the body chamber there are

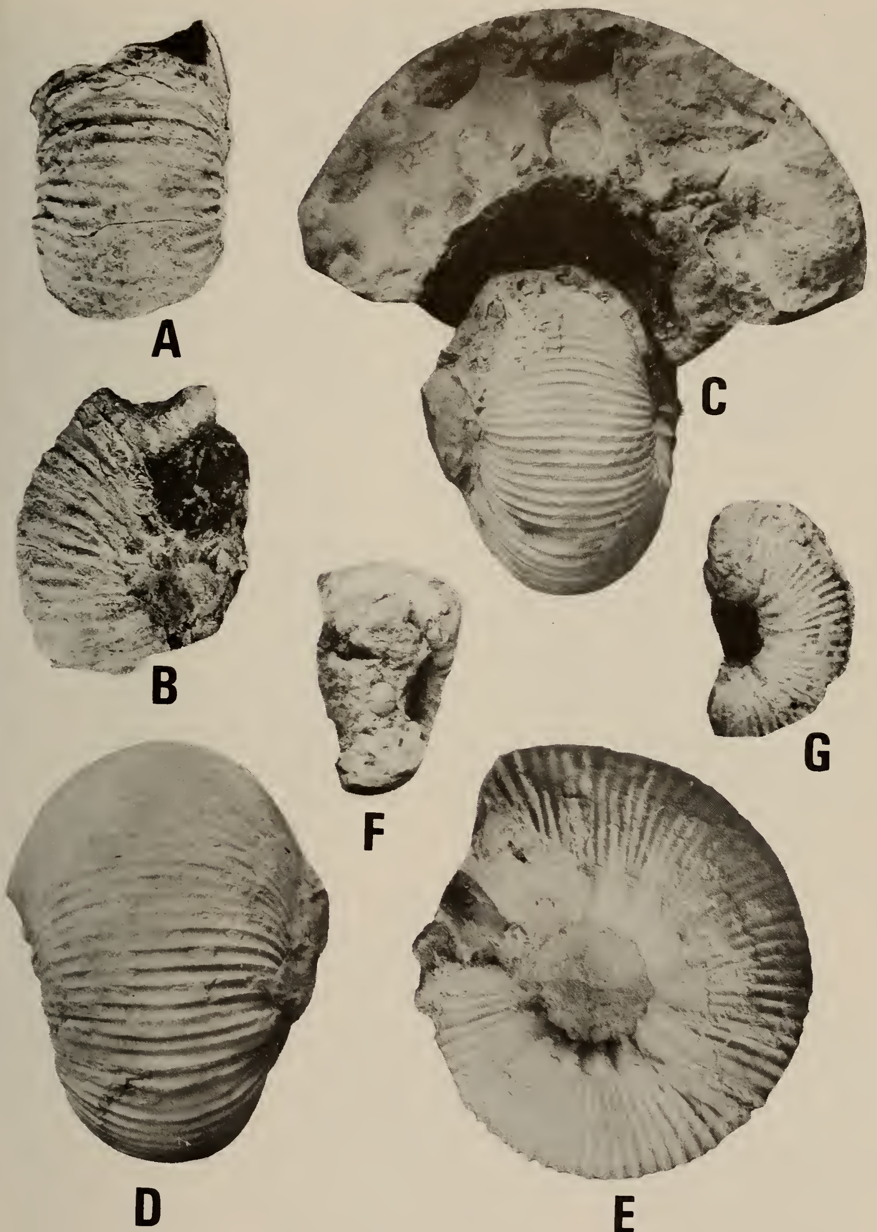

Fig. 144. A–B, F–G. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe). A–B. Ventral and lateral views of SAM–581, a microconch, × 0,75. F–G. Front and lateral views of an immature specimen, SAM–PCU1579, × 0,66. Note fine ribbing and prominent parabola on smooth nucleus. C–E. *Olcostephanus* (*Olcostephanus*) *baini* var. *sphaeroidalis* (Spath) (♀). Front, ventral and lateral views of the holotype of *Rogersites sphaeroidalis* Spath. SAM–9241. × 0,62.

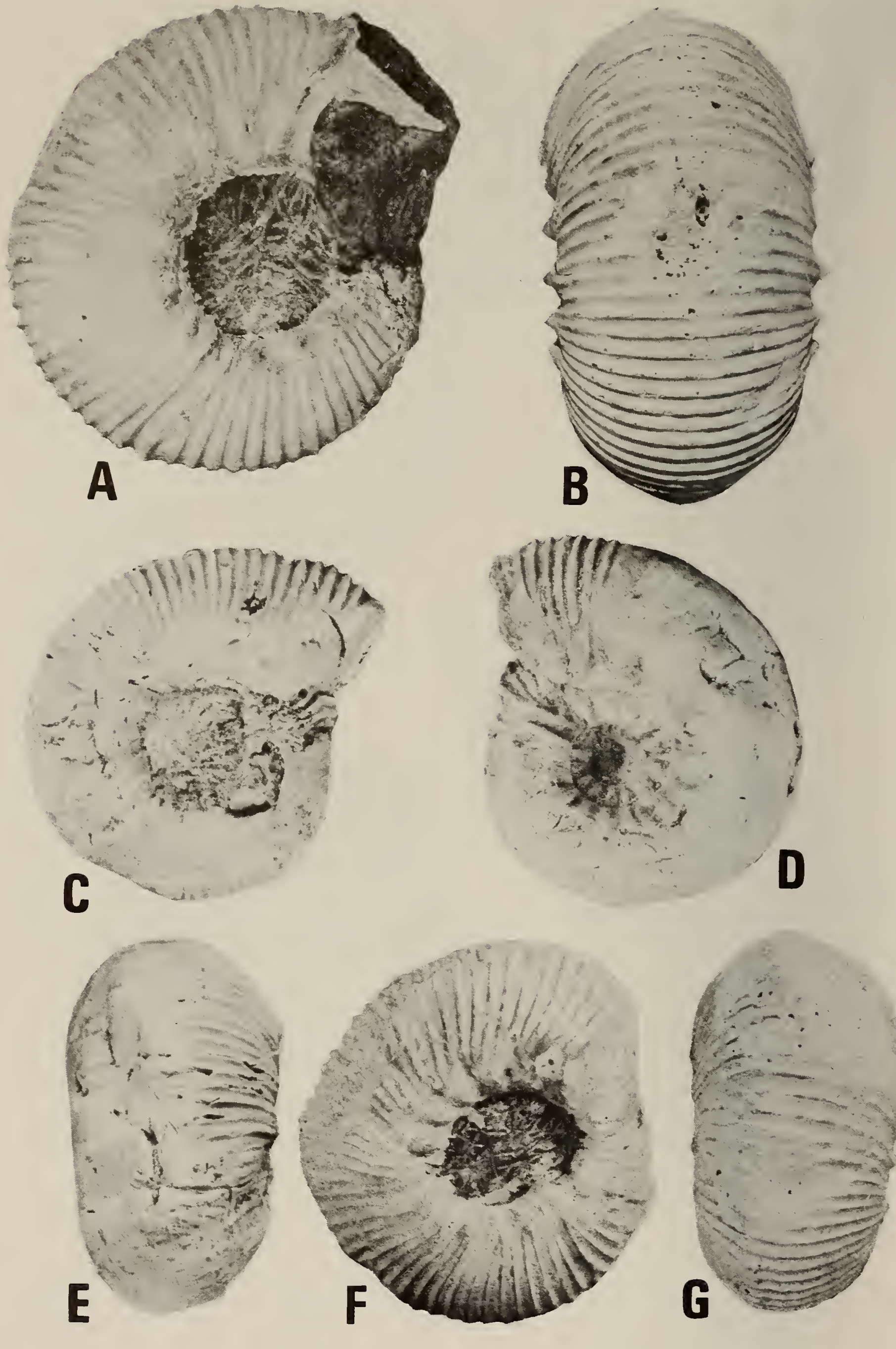

Fig. 145. *Olcostephanus* (*Olcostephanus*) *baini* var. *sphaeroidalis* (Spath) (♂). A–B. Lateral and ventral views of SAM–PCU1592, × 0,75. C–E. Right lateral, left lateral and ventral views of SAM–PCU1534, × 0,75. F–G. Lateral and ventral views of SAM–PCU1575, × 0,66.

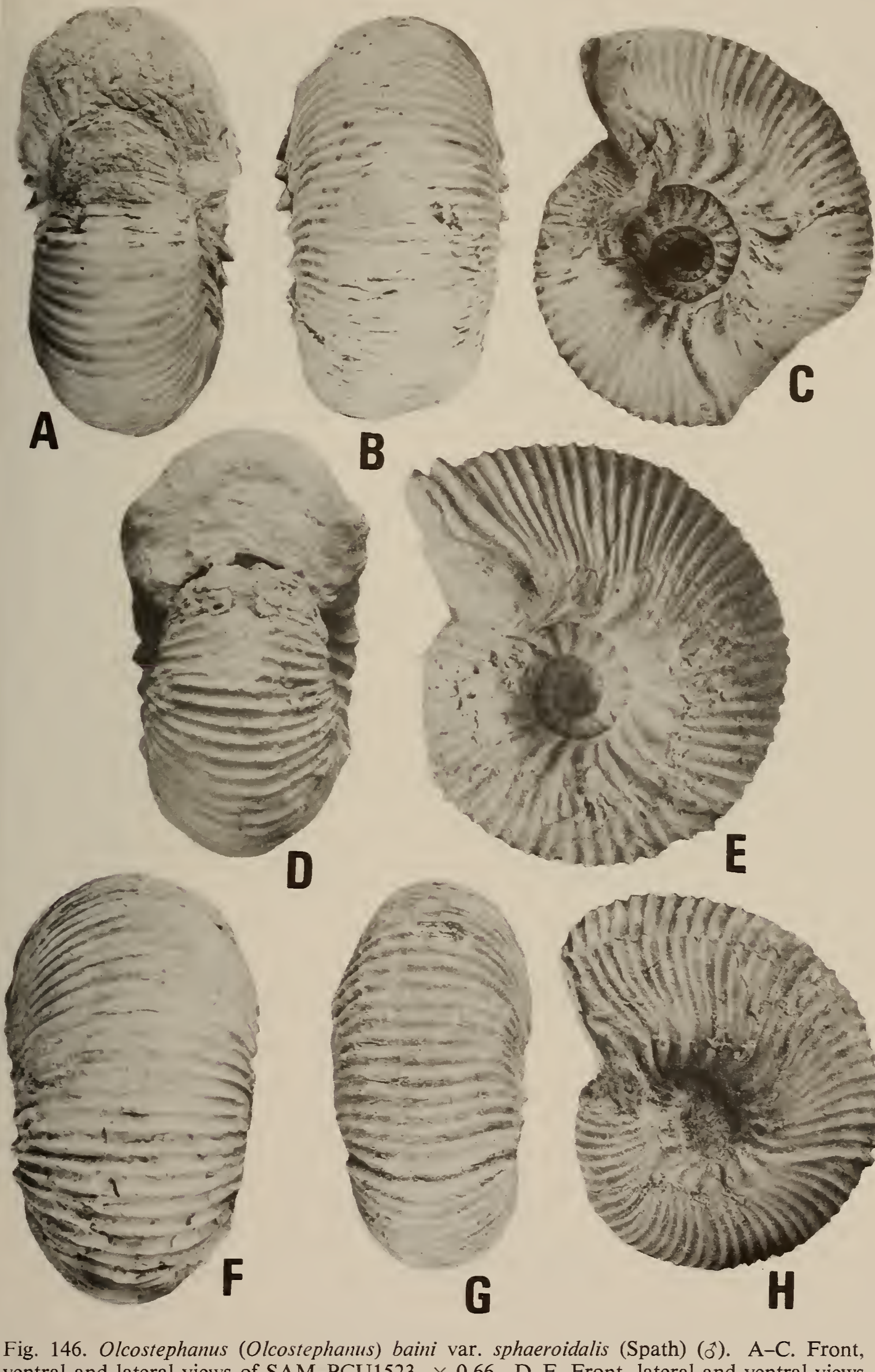

Fig. 146. *Olcostephanus* (*Olcostephanus*) *baini* var. *sphaeroidalis* (Spath) (♂). A–C. Front, ventral and lateral views of SAM–PCU1523, × 0,66. D–F. Front, lateral and ventral views of PEM–1468/76, a specimen transitional to *O. b. baini*, × 0,86. G–H. Ventral and lateral views of SAM–PCU1525, × 0,75.

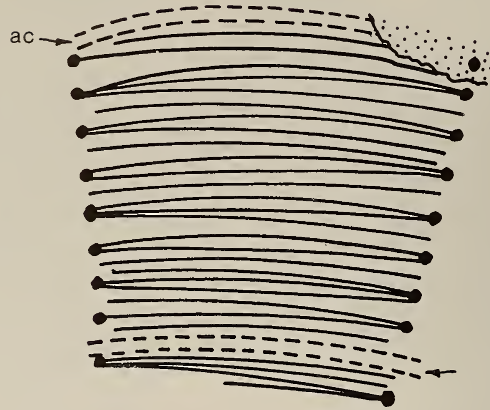

Fig. 147. Schematic representation of the rib pattern of *Olcostephanus* (*Olcostephanus*) *baini* var. *sphaeroidalis* (Spath) (♂) on PEM–1462/76a (ac = apertural constriction).

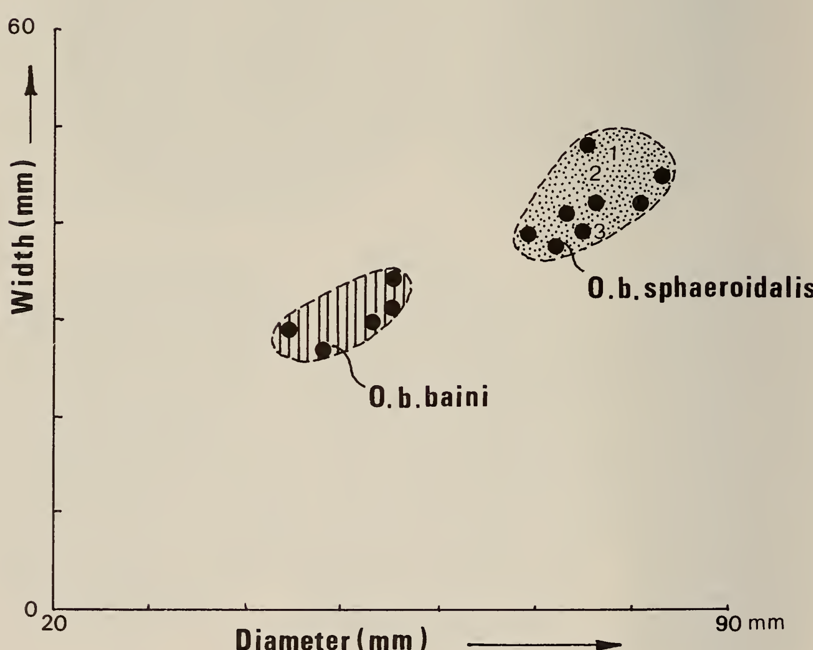

Fig. 148. Diameter/width plot showing the relationship between microconchs of *O. b. bain*, and *O. baini* var. *sphaeroidalis*.

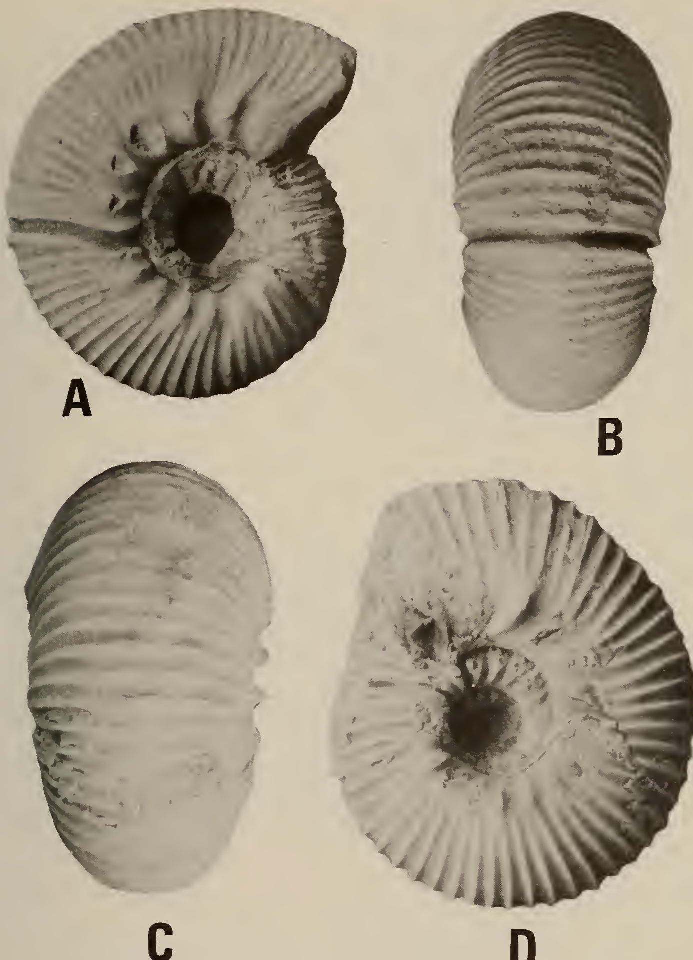

Fig. 149. *Olcostephanus* (*Olcostephanus*) *baini* var. *sphaeroidalis* (Spath) (♂). A–B. Lateral and ventral views of BM–C47133. C–D. Ventral and lateral views of BM–C47131. × 0,75.

12–14 secondaries within a 40 mm distance, with 19–22 secondaries per 5 bullae. There are prominent parabolae on the outer whorl, while the peristome is ornamented with lateral lappets.

Macroconch (♀): as already pointed out, the outer whorls of the macroconch of this variety appear to be indistinguishable from those of *O. baini baini*. Consequently, it is only the inner whorls of this macroconch form that can be recognized. In SAM–9241 (the holotype of *O. sphaeroidalis* (Spath)), which represents an immature macroconch, the whorls are moderately inflated to a diameter of 55 mm, whereafter they increase very rapidly in width to become

extremely inflated and strongly depressed. On the outer whorl, at 68 mm diameter, about 16 rursiradiate primaries terminate in bullae from which bundles of commonly 4, rarely 3 or 5, rather fine, prorsiradiate secondaries arise and recurve slightly so as to cross the venter transversely. There are 26 secondaries per 5 bullae at this growth stage, with 16 ribs in a 40 mm distance along the venter. Beyond this growth stage it seems unlikely that this variety can be distinguished from *O. baini baini* (♀).

Measurements

No.	D	H	Wi	W/H	Uo	Ui
SAM–PCU1593	79	33	43	1,30	40	29 (37) (♂)
SAM–PCU1592	85	36	48	1,33	41	? (♂)
SAM–PCU1596	79	37	51	1,38	35	26 (33) (♂)
SAM–PCU1595	73	33	41	1,24	?	? (♂)
SAM–PCU1523	83	35	42	1,20	40	26 (31) (♂)
,,	64	30	35	1,17	29	18 (28)
SAM–PCU1534	73	32	42	1,31	37	27 (37) (♂)
SAM–PCU1525	70	30	35	1,17	?	? (♂)
PEM–1468/76	68	30	38	1,27	29	18 (26) (♂)
,,	43	20	28	1,40	22	11 (26)
BM–C47133	68	27	34	1,26	34	22 (32) (♂)
,,	53	20	30	1,50	23	15 (28) (♂)
BM–C47131	68	27	35	1,30	32	19 (28) (♂)
SAM–9241	*c.*130	65	110	1,69	?	? (♀)
,,	68	30	47	1,57	28	?
,,	55	24	32	1,33	?	?

Discussion

The microconch of this variety differs from the *O. baini baini* microconch in its larger size (about 70–80 mm diameter as against 50–60 mm), more compressed form, greater number of umbilical bullae (18–22 as against 14–18), and more secondaries per bulla (3–4 as against 2–3). While these differences in the microconchs were at first thought to be of specific value, the fact that the macroconchs can be distinguished only during their early ontogenetic stages suggests that the differences are of no more than varietal importance.

A single example, from the Sundays River Formation, PEM–1468/76 (Fig. 146D–F), appears to be transitional between *O. baini baini* (♂) and *O. baini* var. *sphaeroidalis* (♂). In this specimen the whorl section is coronate at the peristome and thus resembles *O. baini baini* in this respect, while there are eighteen bullae on the final whorl, corresponding to the upper limit of *O. baini baini* but below the average of about twenty for the *O. baini* var. *sphaeroidalis* microconch. Moreover, the ribbing is finer and closer than in typical examples of *O. baini baini*, while its dimensions are within the range of *O. baini* var. *sphaeroidalis*.

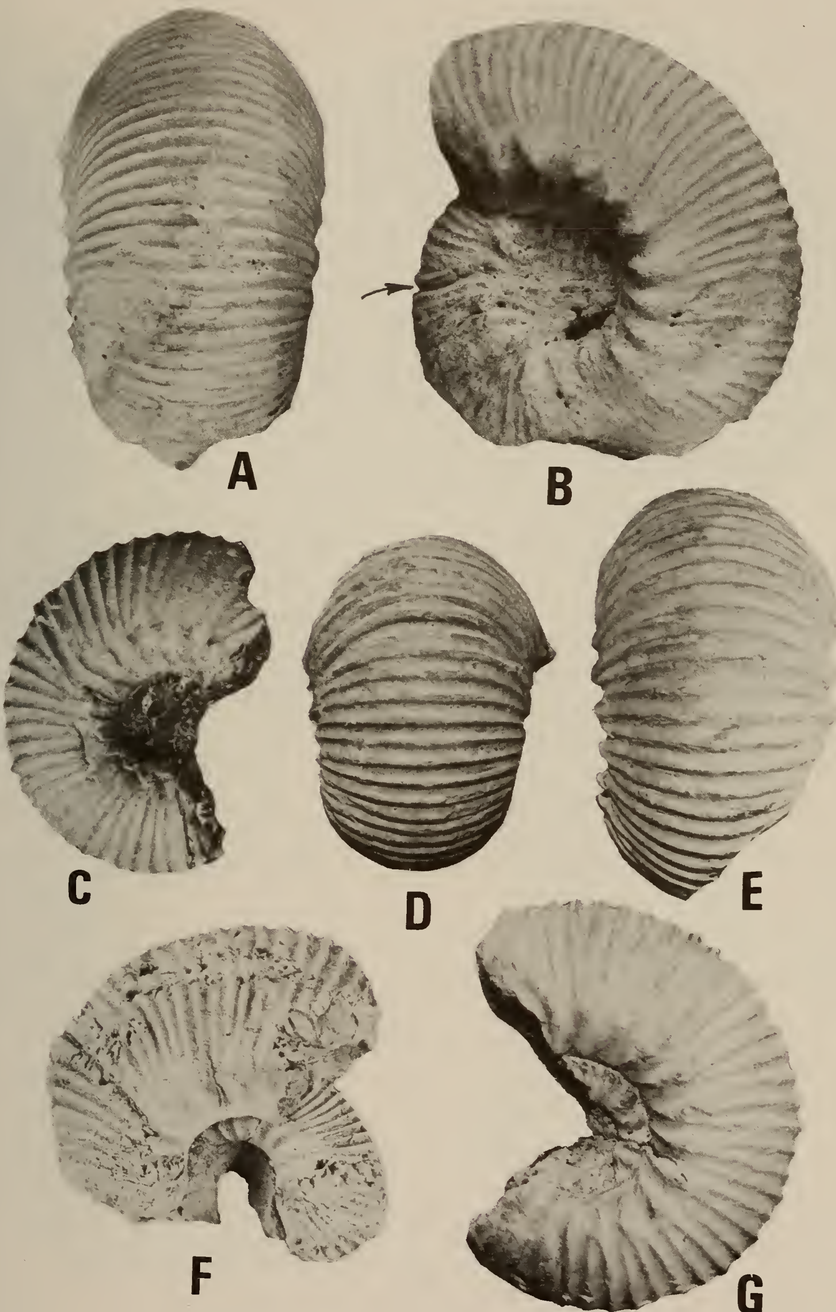

Fig. 150. A–B. *Olcostephanus* (*Olcostephanus*) *baini* var. *sphaeroidalis* (Spath) (♂). Ventral and lateral views of SAM–PCU1592, × 0,75. C–D. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe). Lateral and ventral views of AAS–370, an immature macroconch, × 0,75. E, G. *Olcostephanus* (*Olcostephanus*) cf. *rogersi* (Kitchin) (♂). Ventral and lateral views of PEM–1468/42, × 0,75. F. *Olcostephanus* (*Olcostephanus*) cf. *baini* (Sharpe). Lateral view of SAM–PCU1591, an immature macroconch, possibly referable to the variety *sphaeroidalis* (Spath), × 0,66.

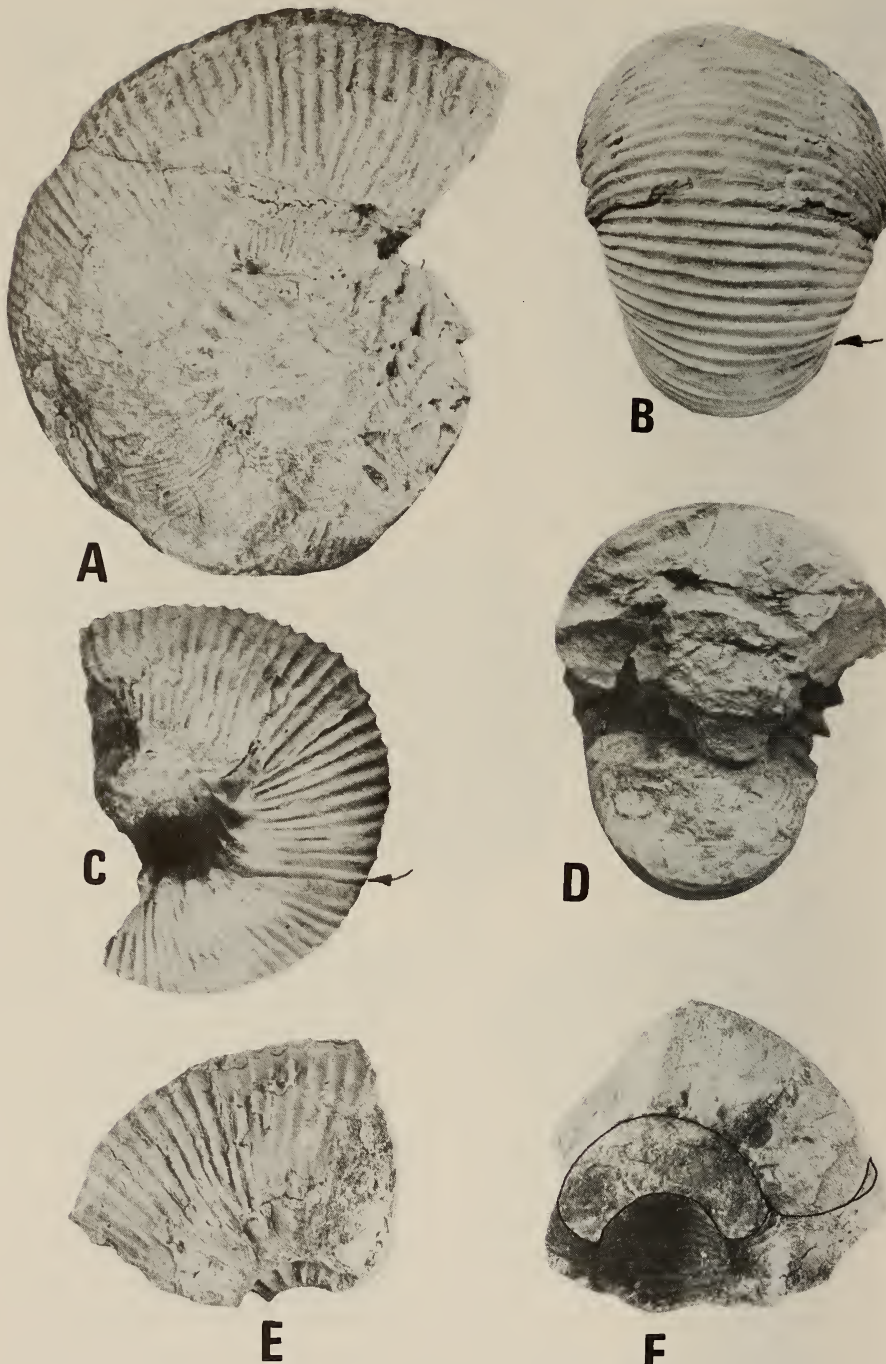

Fig. 151. A. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♀). Lateral view of the crushed inner whorls of SAM–320, × 0,66. B–D. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe) (♀). Ventral, lateral and front views of a specimen in the Albany Museum. Note the increase in inflation immediately after a parabola, × 0,75. E–F. *Olcostephanus* (*Olcostephanus*) cf. *perinflatus* (Matheron) (♀). Lateral and front views of AAS–425. Note the extreme inflation and fine ribbing, × 0,55.

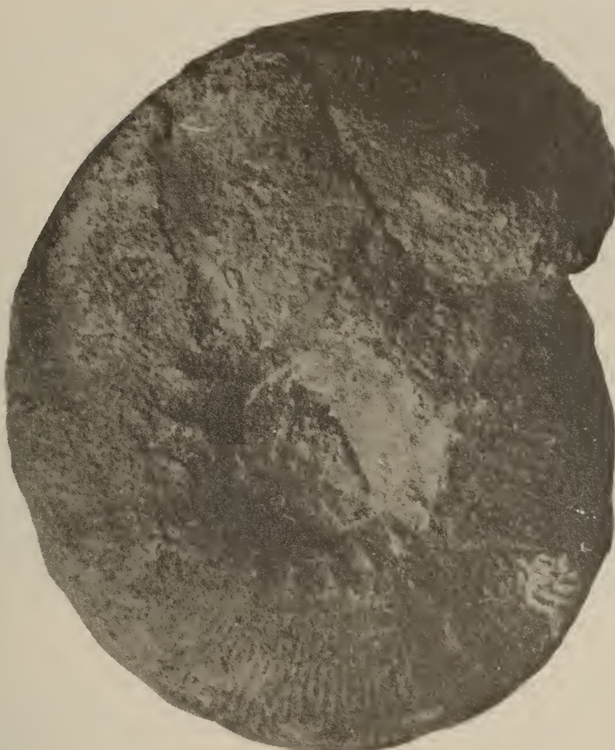

Fig. 152. *Olcostephanus* (*Olcostephanus*) *glaucus* Spath (♀). The holotype from the Spiti Shales of Pakistan. (after Spath 1939). × 1.

As can be seen from Fatmi's (1977) figure and description, *Olcostephanus* (*Rogersites*) *madagascariensis* var. *isakhelensis* Fatmi is a junior subjective synonym of the microconch of this taxon.

Olcostephanus glaucus Spath (1939) (Fig. 152) differs from the present species in being less inflated, more finely and densely ribbed and, in the holotype, lacking constrictions. The constricted paratype (Spath 1939, pl. 6 (fig. 7)) is very close, however, to the microconch of the present variant, and may prove to be identical.

Collignon (1962: 44) considered *O. ankaranensis* (Fig. 153) to be characterized by '. . . ses tours subcylindriques dont l'épaisseur reste à peu près constante, la réduction des flancs qui sont limités a la partie garnie de tubercules ombilicaux, et par un ombilic profond et trés large'. So far as the writer is able to judge, there are no features whereby this species can satisfactorily be separated from the microconch of the present form, of which *O. ankaranensis* (Collignon) thus becomes a probable junior subjective synonym.

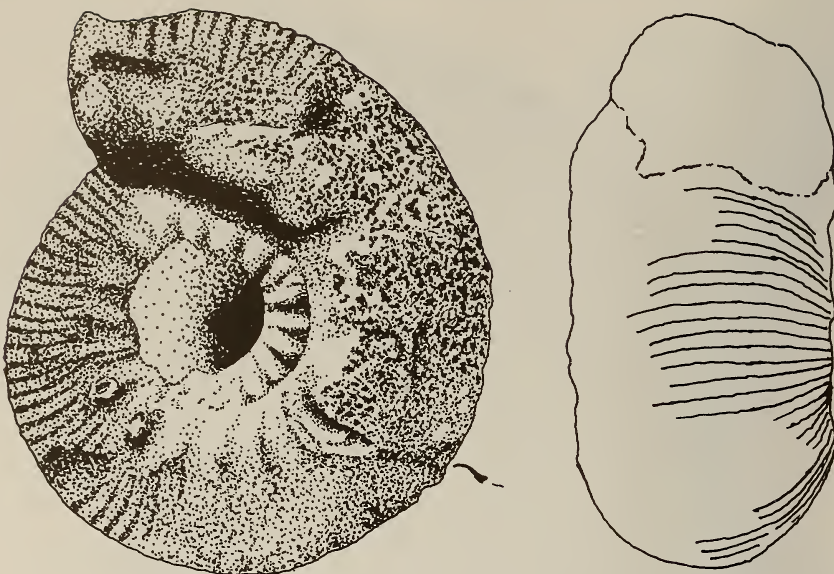

Fig. 153. *Olcostephanus* (*Olcostephanus*) *baini* var. *sphaeroidalis* Spath (♂). The holotype of *Holcostephanus ankaranensis* Collignon from the Upper Valanginian of Ambiky, Madagascar (after Collignon 1962). × 1.

The constricted example of *Astieria leptoplana* figured by Baumberger (1908, pl. 26 (fig. 4)) shows no features satisfactorily to distinguish it from the present material with which it is here included.

Occurrence

This variety is known from the Swiss Jura, Pakistan, Madagascar, South Africa, and possibly Mexico.

Olcostephanus (*Olcostephanus*) *ventricosus* (von Koenen, 1902)

Figs 154–156

Olcostephanus multiplicatus Neumayr & Uhlig (*non* Roemer), 1881: 150, pl. 33 (fig. 2).
Astieria ventricosa von Koenen, 1902: 144. Kitchin, 1908: 189.
? *Astieria convoluta* von Koenen, 1902: 146, pl. 39 (fig. 4a–b).
Astieria rigida Baumberger, 1908: 7, pl. 28 (fig. 1), fig. 121.
Holcostephanus (*Astieria*) *ventricosus* (von Koenen) Wegner, 1909: 87.

Material

Two specimens, LJE–989a, SAM–PCU1607.

Holotype

The original of *Olcostephanus multiplicatus* Römer (Fig. 155) figured by Neumayr & Uhlig (1881: 150, pl. 33 (fig. 2)) from Höheneggelsen, northern Germany.

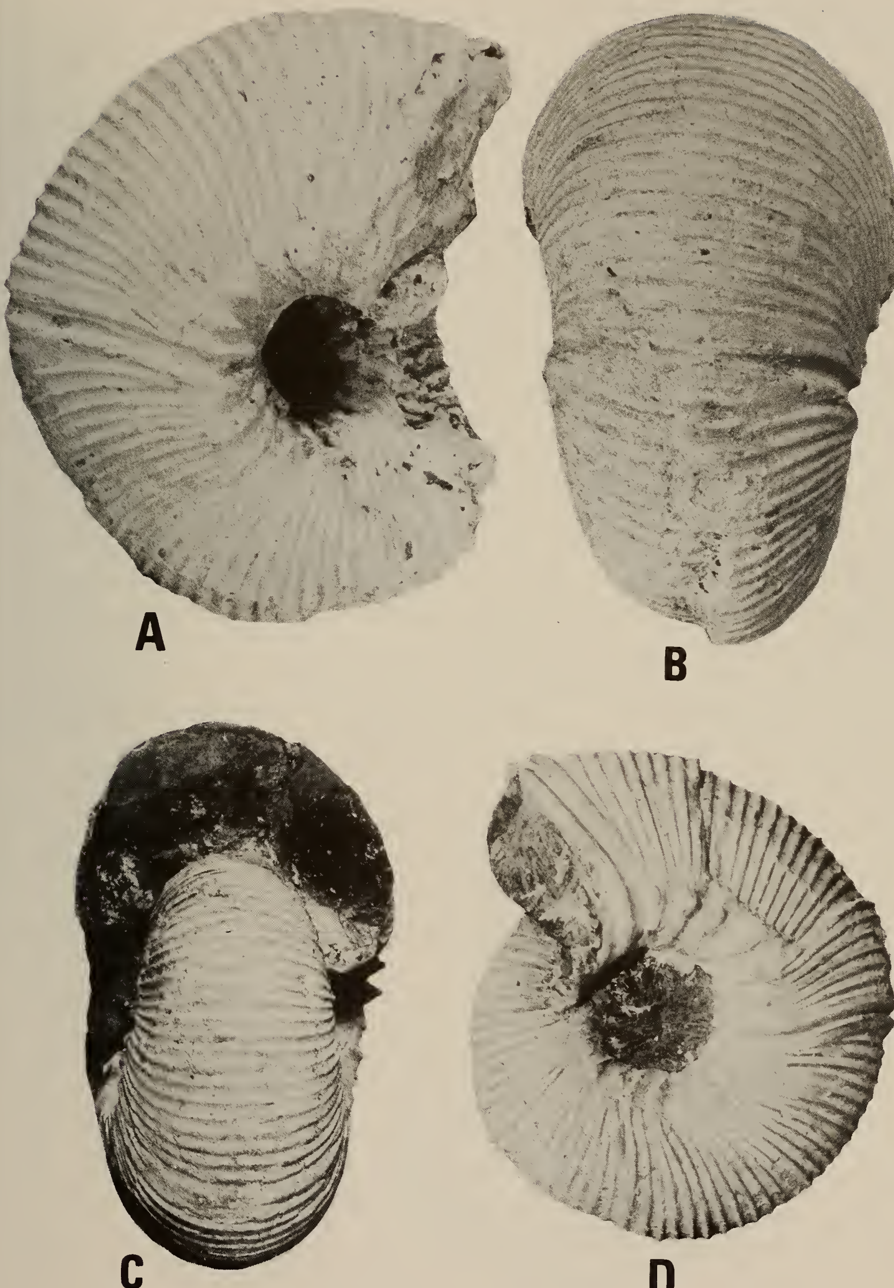

Fig. 154. *Olcostephanus* (*Olcostephanus*) *ventricosus* (von Koenen), × 0,75. Lateral and ventral views of SAM–PCU1607. C–D. Front and lateral views of LJE–989*a*.

Diagnosis

Medium-sized, somewhat inflated, with a semicircular whorl section. About 18–22 rursiradiate primaries terminating in sharp bullae, from which arise 2–4, commonly 3, prorsiradiate, slightly flexuous, secondaries. Prominent deep parabolae present. Possibly the inner whorls of a macroconch.

Description

Two specimens from the Sundays River beds, one rather crushed, are referable to this species. LJE–989a has the recrystallized test preserved, and closely resembles the type figured by Neumayr & Uhlig.

This example is somewhat inflated and moderately large. It is involute up to the umbilical bullae and has a steep umbilical wall. The whorl section is depressed, with an almost perfectly semicircular whorl section. Distinctly rursiradiate primaries terminate in 20 sharp bullae on the umbilical shoulder of the outer whorl. These in turn give rise to 2–4, commonly 3, prorsiradiate secondaries which recurve slightly on the upper part of the flanks so as to cross the venter transversely. There are 25 secondaries per 7 bullae on the adapical portion of the outer whorl (about 65 mm diameter) and 24 per 6 bullae on the adoral portion. There are invariably 1–2 intercalated ribs between bundles, with 11 secondaries within a 30 mm distance along the venter of the outer whorl. The outer whorl is ornamented with 2 prominent parabolae.

SAM–PCU1607 is very similar, but rather crushed at the adapical portion of the outer whorl. This specimen would appear to have part of a peristome preserved, but there are no signs of lateral lappets.

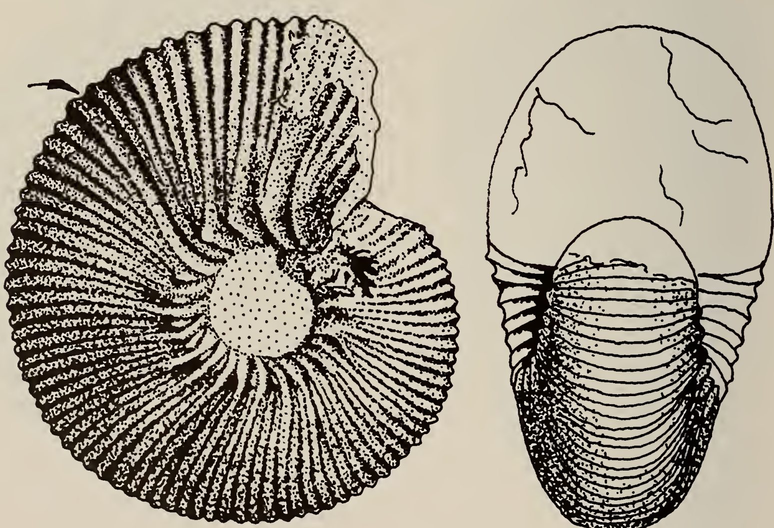

Fig. 155. *Olcostephanus* (*Olcostephanus*) *ventricosus* (von Koenen). The holotype of *Astieria ventricosa* von Koenen, from north-west Germany (after Neumayr & Uhlig 1881). × 1.

Measurements

No.	D	H	Wi	W/H	Uo	Ui
LJE–989a	80	27	44	1,63	26	14 (18)
,,	60	23	33	1,43	25	12 (20)
,,	45	17	23	1,35	17	8 (18)
SAM–PCU1607	109	53	64	1,21	34	21 (19)

Discussion

This is a rather problematical form since it is uncertain whether it represents the inner whorls of a macroconch, or if it is a large microconch species. Its large size would seem to favour the former, whilst its lack of inflation suggests the latter.

This species is clearly very closely related to *O. baini* from which it seems to differ only in remaining relatively compressed to large diameters.

According to Von Koenen (1902), *Astieria convoluta* is a moderately inflated form with a deep, narrow umbilicus. Rursiradiate primaries terminate on the umbilical shoulder in bullae, of which there are about 8 per half whorl. There are generally 3 prorsiradiate secondaries per bulla, with an intercalated rib between bundles, and a prominent parabola on the outer whorl. There is little to separate this species from *O. ventricosus*, of which it may prove to be a junior subjective synonym.

Astieria dalpiazi Rodighiero (1919) was compared with *O. ventricosus* but has never been figured. It was said to have short, weak, thin primary ribs which terminate in tubercles on the umbilical shoulder from which arise 2–3 secondary ribs. The secondaries bifurcate at various levels on the flanks so that 4–6 ribs cross the venter for each tubercle. Parabolae are present. According to Rodighiero (1919), '*A.*' *dalpiazi* differs from *O. ventricosus* in being more inflated, with a narrower, deeper umbilicus. However, Von Koenen's (1902) species does not have bifurcating secondaries and is probably specifically distinct.

Olcostephanus rigidus (Baumberger) (Fig. 156) does not appear to be specifically distinct from this form, and supports its treatment as the inner whorls of a macroconch. Baumberger's species was erected for moderately inflated forms with 23–24 rursiradiate primaries on the outer whorl, each terminating in umbilical bullae from which arise bundles of 3–4 prorsiradiate secondaries commonly with 2 intercalated ribs between bundles. There is a prominent parabola on the outer whorl. The whorl section is semicircular. Thus, there is no significant feature by which this species can be distinguished from *O. ventricosus* and they should be considered conspecific.

Since the outer whorls of this probable macroconch form are unknown, as is the microconch dimorph, its true status is not known, and must await study of topotype material.

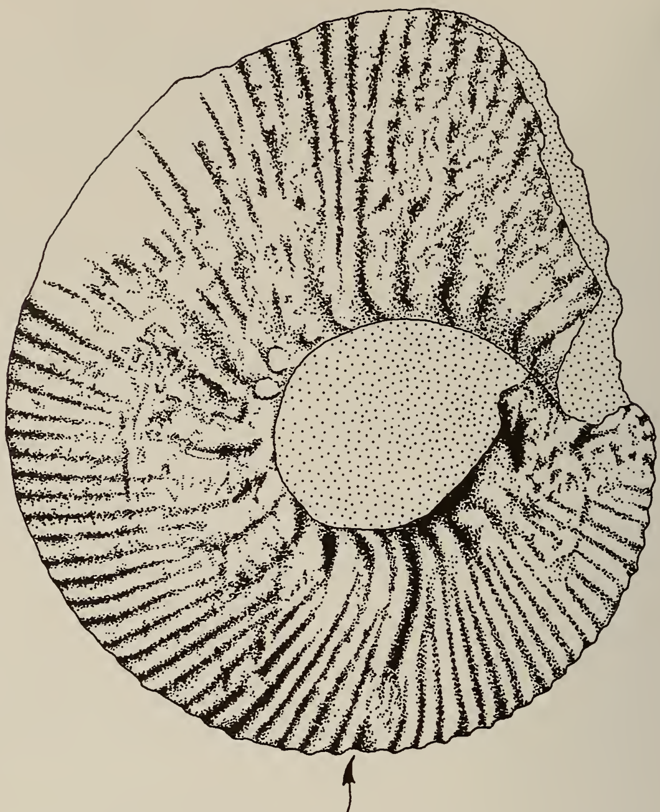

Fig. 156. *Olcostephanus* (*Olcostephanus*) *ventricosus* (von Koenen). The lectotype, designated herein, of *Astieria rigida* Baumberger, from the Swiss Jura (after Baumberger 1908). × 1.

Occurrence

This species is known from the Swiss Jura, northern Germany, South Africa, the south of France, and possibly Tanzania.

Olcostephanus (*Olcostephanus*) *uitenhagensis* (♀) (Kitchin, 1908)
Figs 157, 158C–D, 159, 160C–D

Holcostephanus uitenhagensis Kitchin, 1908: 206, pl. 11.
Holcostephanus (*Astieria*) *uitenhagensis* Kitchin, Wegner, 1909: 89. Kilian, 1910: 214.
Holcostephanus uitenhagensis Kitchin, Hatch & Corstorphine, 1909: 295, fig. 73 (right-hand specimen only).
Rogersites uitenhagensis (Kitchin) Spath, 1930: 150. Besairie, 1936: 141.
Olcostephanus uitenhagensis (Kitchin) Spath, 1939: 19. Riccardi *et al*., 1971: 90. Reyment & Tait, 1972: 60.

Material

Three specimens, all macroconchs (SAM–5069, SAM–PCU1524, SAM–PCU1605).

Fig. 157. *Olcostephanus* (*Olcostephanus*) *uitenhagensis* (Kitchin) (♀). Lateral and front views of the holotype, SAM–5069, a poorly preserved internal mould. × 0,55.

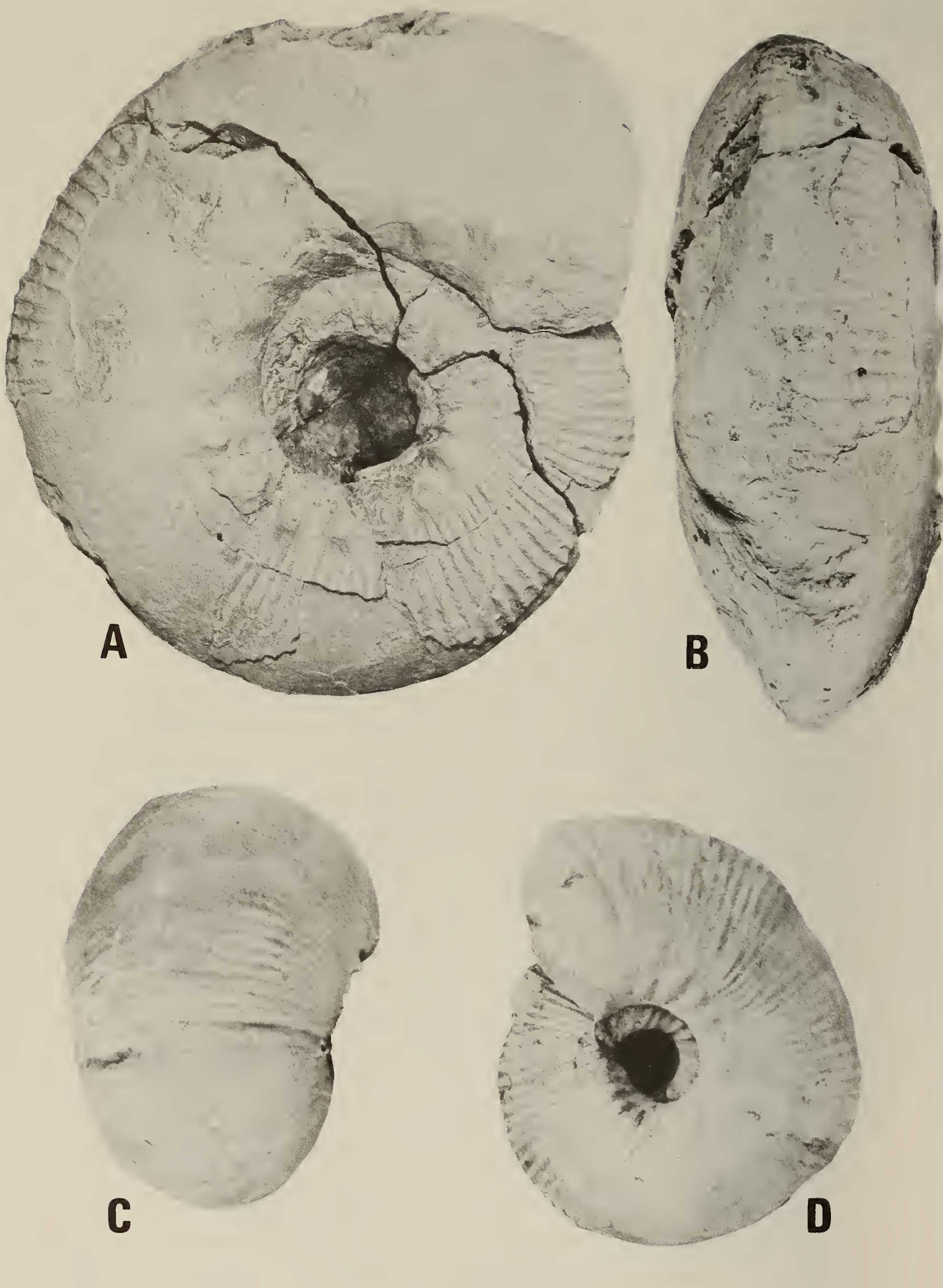

Fig. 158. A–B. *Olcostephanus* (*Olcostephanus*) *uitenhagensis* (Kitchin) (♀). Lateral and ventral views of SAM–PCU1605, retaining patches of recrystallized test. × 0,44. C–D. *Olcostephanus* (*Olcostephanus*) sp. (♀). Ventral and lateral views of SAM–PCU1531. Note fine, flexuous ribbing and parabola. × 0,55.

Holotype

By monotypy, the original of *Holcostephanus uitenhagensis* Kitchin (1908: 206, pl. 11) (Fig. 157) from '. . . between milestones 24½–24¾ on the Graaff-Reinet railway, about three miles from Uitenhage'. The holotype, SAM–5069 is in the South African Museum.

Diagnosis

Large (about 200 mm diameter), compressed macroconchs which become markedly evolute on the final whorl. Flanks prominent, steep and slightly convex. On the penultimate whorl rursiradiate primaries terminate in 19 bullae on the umbilical shoulder. On the final whorl the primaries become very weak, disappearing entirely on the internal mould, and the tubercles become swollen and rounded, as well as fewer (15) in number. Flexuous prorsiradiate secondaries arise in bundles of 3–5, with 1–2 intercalated ribs between bundles. Parabolae lacking, on outer whorls at least. Peristome simple.

Description

Only macroconchs of this species have been described, and until the ontogenetic variation is known it is highly unlikely that the microconch dimorphs will be recognized.

The shell is a large, compressed cadicone, involute up to the umbilical bullae except on the last two-thirds of the body chamber when the umbilical seam egresses rapidly and the final whorl becomes about 30 per cent evolute at the peristome. The umbilicus is fairly narrow and rather deep, with vertical umbilical walls on the inner whorls and an acute umbilical shoulder. On the body chamber, with the egression of the umbilical seam, the slope of the umbilical wall decreases markedly and the shoulder becomes rounded.

Also with the egression of the umbilical seam, the prominent rursiradiate primaries weaken considerably and are almost entirely effaced on the adoral portion of the final whorl. At the same time, the distinctly bullate umbilical tubercles of the penultimate whorl become swollen and rounded. There are 15 umbilical tubercles on the body chamber, whereas the penultimate whorl is ornamented with 19 bullae.

Specimen SAM–PCU1524 is a well-preserved example of this species which, unlike the holotype which represents an internal mould, has the recrystallized test preserved. Unfortunately it has been slightly crushed laterally.

On this example, the secondary ribbing is rather fine and slightly prorsiradiate, becoming distinctly coarser and more inclined near the peristome. On the penultimate whorl the secondaries are slightly flexuous, arising radially from the umbilical bullae only to curve forward low down on the flanks and then gently recurve so as to cross the venter transversely. On the penultimate whorl there are 16 secondaries per 3 bullae, while on the adoral portion of the body chamber there are 25, with 13 ribs within a 60 mm distance along the

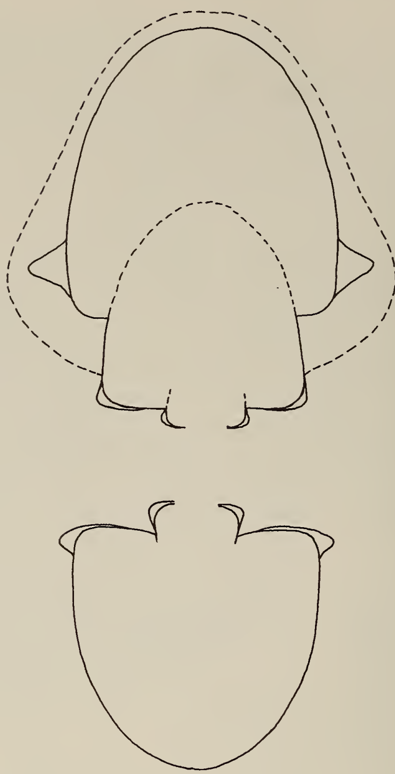

Fig. 159. *Olcostephanus* (*Olcostephanus*) *uitenhagensis* (Kitchin) (♀). Whorl section of SAM–PCU1524. Dotted line represents shape of the final peristome. × 0,5.

venter. Parabolae are lacking on the outer whorls, although the peristome is strongly constricted, cutting obliquely across 4 ribs to the posterior, and with a prominently flared adapical margin.

Measurements

No.	D	H	Wi	W/H	Uo	Ui
SAM–5069	225	88	*c.*93	1,11	87	67 (30)
,,	*c.*155	69	82	1,19	49	37 (24)
SAM–PCU1524	188	71	*c.*71	1,00	74	51 (27)
,,	155	67	*c.*64	0,96	52	35 (22)

Discussion

Olcostephanus uitenhagensis is a macroconch characterized by the marked egression of the umbilical seam on the final whorl, its compressed form, and the change in the nature of the tuberculation on the body chamber.

Olcostephanus of the *astierianus* plexus do not show the marked egression

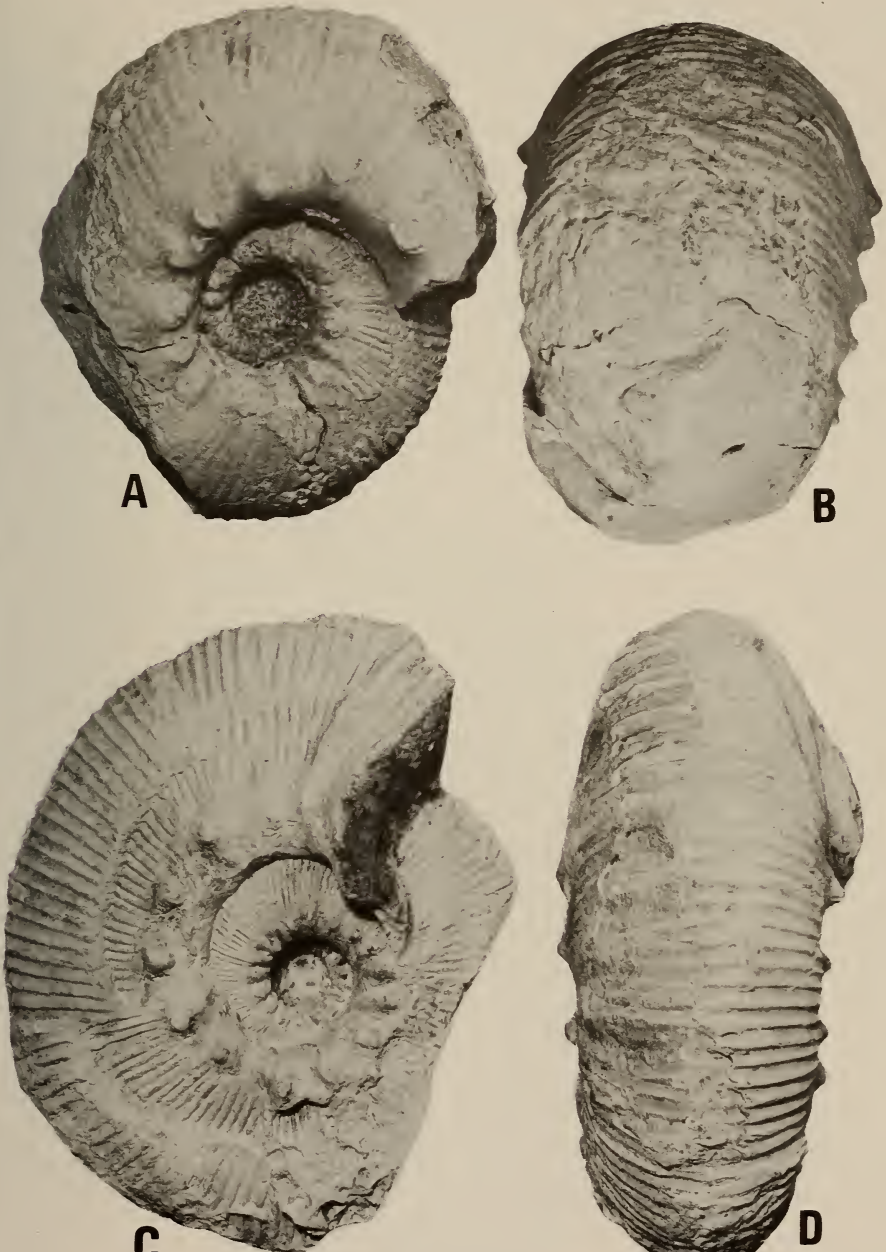

Fig. 160. A–B. *Olcostephanus* (*Olcostephanus*) *riccardii* sp. nov. (♀). Lateral and ventral views of the holotype, SAM–PCU1577. Note inflated form, lack of parabolae and rounded umbilical tubercles on the body chamber. × 0,44. C–D. *Olcostephanus* (*Olcostephanus*) *uitenhagensis* (Kitchin) (♀). Lateral and ventral views of SAM–PCU1524. Note compressed form, egression of the umbilical seam, rounded tubercles on the body chamber and constricted peristome. × 0,44.

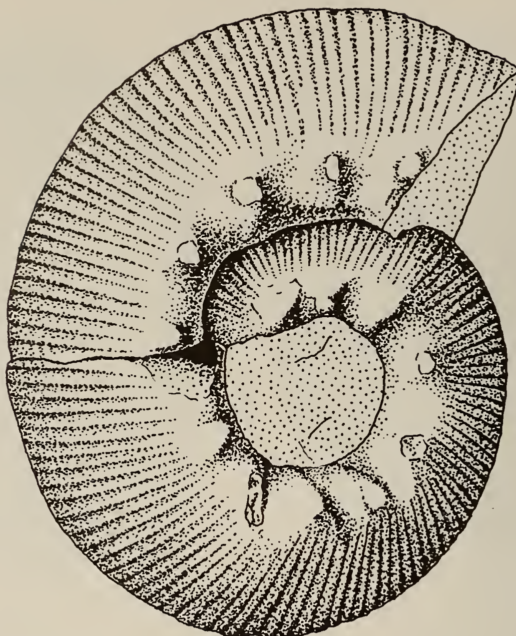

Fig. 161. *Olcostephanus* (*Olcostephanus*) *singularis* (Baumberger). The lectotype, designated herein, from the Swiss Jura (after Baumberger 1908). × 1.

of the umbilical seam displayed by *O. uitenhagensis* in maturity, as well as commonly retaining bullate umbilical tubercles to the peristome.

Olcostephanus singularis (Baumberger) (Fig. 161) is the closest species to *O. uitenhagensis*. It has a moderately inflated shell with a strongly depressed whorl section and shows marked egression of the umbilical seam on the outer (?final) whorl. About 12, rounded, swollen, umbilical tubercles on the outer whorl give rise to bundles of 5–6 slightly prorsiradiate secondaries, between which are 2–3 intercalated ribs. Parabolae are lacking. This species differs from *O. uitenhagensis* in that the umbilical tubercles are swollen and rounded even on the inner whorls as witnessed by *O. klaatschi* (Wegner) which is merely based upon a juvenile of Baumberger's (1908) species.

Olcostephanus rabei (Besairie) (Fig. 69A–B), as noted by Besairie (1936), is indeed very close to the inner whorls of *O. uitenhagensis*. However, without knowledge of the final whorls, the true affinities of *O. rabei* are obscure as it also closely resembles *O. sakalavensis*.

Occurrence

This species has been known with certainty only from South Africa, although Reyment & Tait (1972) have recently reported its occurrence in Argentina.

Olcostephanus (Olcostephanus) riccardii sp. nov.

Figs 162–163

Material

Two specimens, SAM–PCU1577 and BM–C47130, of which the former is designated as the holotype, and the latter is a paratype.

Holotype

SAM–PCU1577 from the Algoa Brick & Tile quarries at Coega.

Diagnosis

A strongly inflated, globose species of *Olcostephanus* with a very depressed whorl section and a deep, narrow umbilicus. Inner whorls with about nineteen umbilical bullae becoming swollen and rounded on the body chamber. Parabolae lacking.

Fig. 162. *Olcostephanus (Olcostephanus) riccardii* sp. nov. (♀). Lateral view of the paratype, BM–C47130. × 0,44.

Etymology

For Dr A. C. Riccardi of the Museo de Ciencias Naturales, La Plata, Buenos Aires, in appreciation of his help in providing literature and constructive criticism of the original manuscript.

Description

The holotype is a strongly inflated, globose cadicone with a narrow umbilicus and steep umbilical walls. The whorls, involute up to the umbilical bullae on the inner whorls, become rather evolute on the adoral portion of the outer whorl. Distinct primaries begin at the umbilical seam and pass backwards (rursiradiate) to 19 bullae on the sharp umbilical shoulder. On the outer whorl the bullae become swollen and distinctly rounded and the primaries are effaced (on the internal mould). There are about 15 tubercles on the final whorl.

On the penultimate whorl secondary ribbing arises in slightly prorsiradiate bundles of 3–4 ribs, commonly with an intercalated rib between bundles, so that there are 17 ribs per 4 bullae. The secondaries recurve slightly so as to cross the venter transversely. On the adoral portion of the body chamber there are 28 secondaries per 4 bullae, with 8 ribs in a 40 mm distance along the venter, whereas on the adapical portion of the outer whorl there are 10 secondaries within a similar distance.

The peristome is not preserved, but the inflated shell leaves little doubt that this form represents a macroconch.

Measurements

No.	D	H	Wi	W/H	Uo	Ui
SAM–PCU1577	150	62	94	1,52	60	45 (30)
,,	110	50	83	1,66	39	26 (24)
BM–C47130	182	77	?	?	80	52 (29)

Discussion

The ornament of this species is almost identical to that of the holotype of *O. uitenhagensis*, the only difference being that whereas Kitchin's type, together with further topotype material, has a noticeably compressed form, this taxon is distinctly inflated and globose. To admit extremely inflated and strongly compressed individuals into the same dimorph would so drastically alter the taxonomy of the group that present evidence does not justify such a move, and hence a new species is created for the present material.

The inner whorls of this species may be distinguished from *O. atherstoni* (♀) by their much greater inflation, and more depressed whorl section.

Mature *O. baini* macroconchs attain a much larger size than this species, while the tubercles remain bullate to the peristome. Moreover, *O. riccardii* does not show the decrease in inflation near the peristome which characterizes *O. baini* macroconchs. Immature examples of *O. baini* (♀) differ in having parabolae.

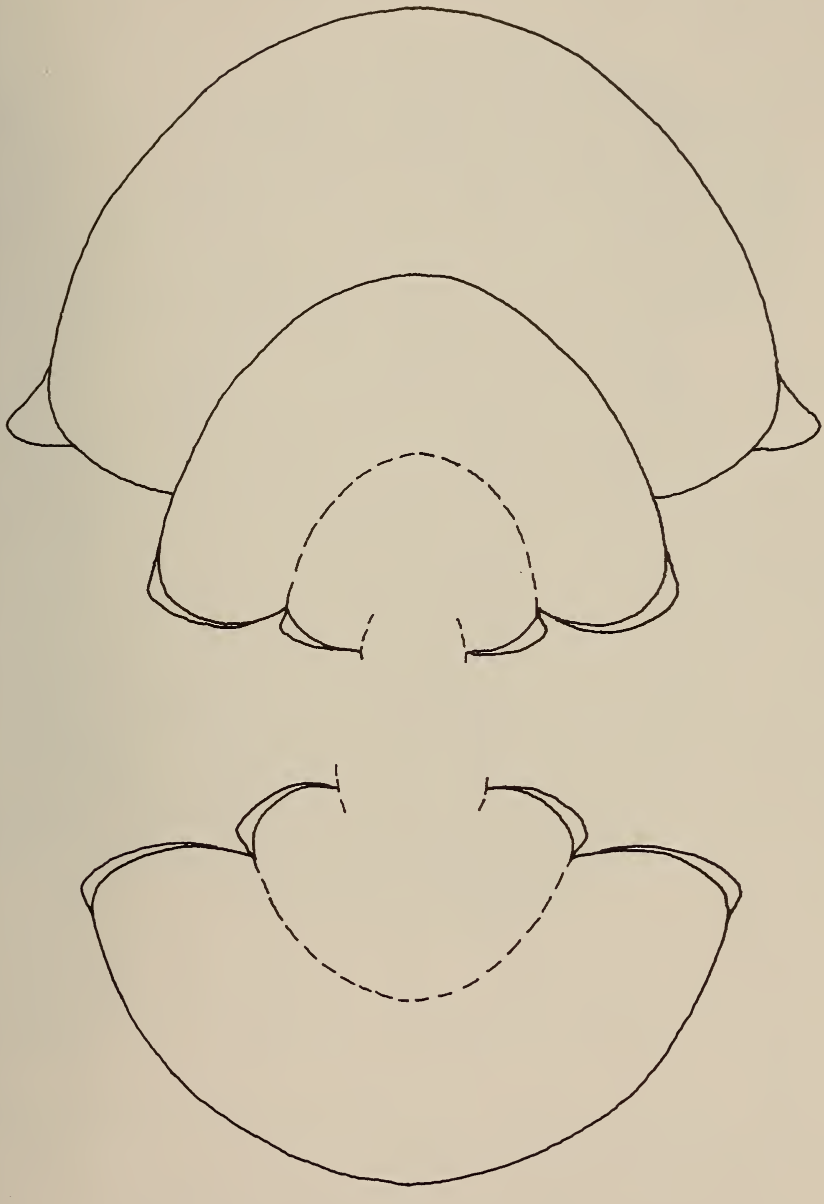

Fig. 163. *Olcostephanus* (*Olcostephanus*) *riccardii* sp. nov. (♀). Whorl section of the holotype, SAM–PCU1577. × 1.

Olcostephanus perinflatus (Matheron) is close to the inner whorls of *O. riccardii* but has radial secondaries, and retains bullate tubercles on to the body chamber.

Occurrence

This species is known only from the Sundays River Formation.

Olcostephanus (*Olcostephanus*) sp.

Fig. 158C–D

Material

A single specimen, SAM–PCU1531, representing an immature macroconch.

Description

A moderately large, strongly inflated cadicone, involute up to the umbilical bullae at all stages on the outer whorl which includes the body chamber. The umbilicus is very narrow and crater-like, with steep convex walls and subangular shoulders. Rursiradiate primaries begin at, or close to, the umbilical seam and terminate in 19 small bullae on the umbilical shoulder of the outer whorl. Each bulla gives rise to bundles of 3–4 fine secondaries, often with an intercalated rib between bundles. On the adapical portion of the outer whorl, however, the nature of the secondary ribbing changes significantly. The secondaries become noticeably finer and distinctly flexuous. From the bullae the secondaries are directed radially for a short distance, before curving forwards to become slightly prorsiradiate and finally recurving so as to cross the venter transversely. There are 17 ribs per 4 bullae on the adoral portion of the outer whorl, with 10 secondaries within a 30 mm distance along the venter. Two indistinct parabolae, due to the fact that the outer whorl is preserved as an internal mould, are present on the body chamber. The whorl section is strongly depressed with a broad, rounded venter.

Measurements

No.	D	H	Wi	W/H	Uo	Ui
SAM–K1531	93	41	67	1,63	33	19 (20)

Discussion

This example differs from *O. baini* macroconchs at a similar diameter by its finer, more flexuous secondary ribbing.

Olcostephanus (*Olcostephanus*) *astieriformis* (Böse, 1923) (♀)

Figs 164–169

Astieria astieriformis Böse, 1923: 72, pl. 1 (figs 1–4). Riedel, 1938: 13.
Olcostephanus astieriformis (Böse) Imlay, 1938: 553.

Fig. 164. *Olcostephanus* (*Olcostephanus*) *astieriformis* (Böse) (♀). Lateral view of a slightly crushed specimen, BM–C47129. × 0,44.

Fig. 165. *Olcostephanus* (*Olcostephanus*) *astieriformis* (Böse) (♀). Lateral view of BM–C47132. × 0,44.

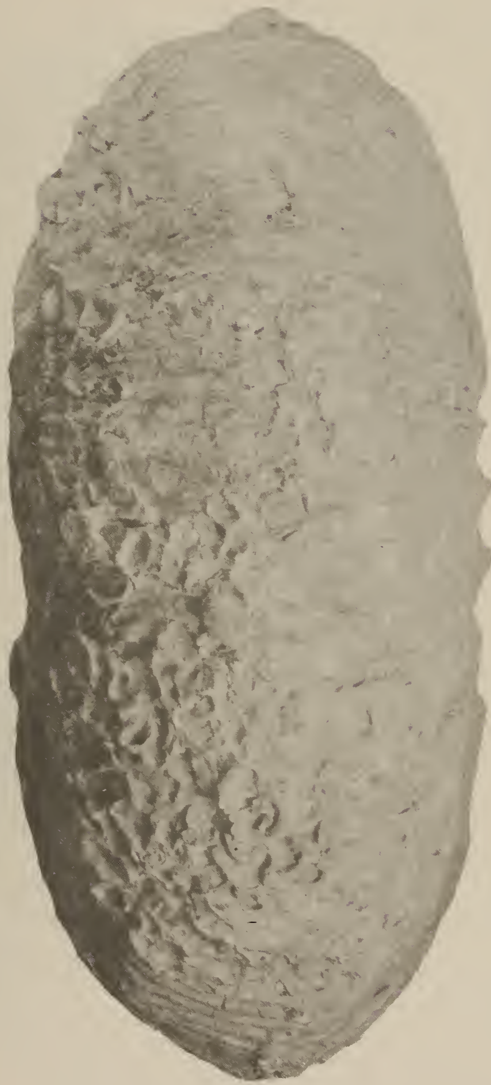

Fig. 166. *Olcostephanus* (*Olcostephanus*) *astieriformis* (Böse) (♀). Ventral view of BM–C47132. × 0,44.

Fig. 167. *Olcostephanus* (*Olcostephanus*) *astieriformis* (Böse) (♀). Lateral and ventral views of a specimen in the South African Museum. × 0,58.

Material

Nine crushed and fragmentary specimens, all macroconchs (BM–C47132, BM–C47129, BM–C47125, SAM–PCU1555, SAM–PCU1541, SAM–PCU1554 SAM–PCU1558, SAM–PCU1553, SAM–PCU1557).

Holotype

By monotypy, the original of *Astieria astieriformis* Böse (Fig. 168), from Durango-Zacatecas, northern Mexico.

Description

A rather variable collection of compressed macroconchs belong here, as well as showing affinities to numerous other nominal species (Figs 169–170).

They are all compressed and show little or no egression of the umbilical seam of the body chamber. The primary ribs are rursiradiate, terminating in 16–25 bullae on the umbilical shoulder from which arise commonly 3–4 prorsiradiate secondaries, usually with intercalatories between bundles. The secondaries very occasionally bifurcate. Parabolae are lacking on the outer whorls, at least, while the inner whorls are currently unknown.

The best preserved example from the Sundays River Formation assignable to this species is BM–C47132. It is an extremely large macroconch (diameter 275 mm) which shows only slight egression of the umbilical seam of the final whorl. The shell is rather compressed, with a narrow deep umbilicus and vertical umbilical walls. The latter are ornamented with 18 rursiradiate primaries terminating in prominent bullae from which bundles of 4–6, fewer at earlier growth stages, flexuous secondaries arise. There is invariably 1–2 intercalatories between bundles. On the adoral portion of the body chamber there are 37 secondaries per 5 bullae, whereas on the adapical portion there are only 23. Parabolae appear to be lacking.

A second example, SAM–PCU1555, is a moderately large (190 mm diameter), compressed cadicone which shows virtually no egression of the umbilical seam on the final whorl. Primary ribs begin at the umbilical seam and pass backwards (rursiradiate) to 17 bullae on the umbilical shoulder, from which 3–5 slightly flexuous, prorsiradiate secondaries arise. There is commonly an intercalated rib between bundles. On the adoral portion of the final whorl there are 18 secondaries per 3 bullae, with a rib spacing of 6 mm. The whorl section is about as wide as high.

Measurements

No.	D	H	Wi	W/H	Uo	Ui
BM–C47132	275	120	125	1,04	94	74 (27)
,,	220	100	?	?	70	54 (25)
SAM–PCU1555	190	87	?	?	70	50 (26)

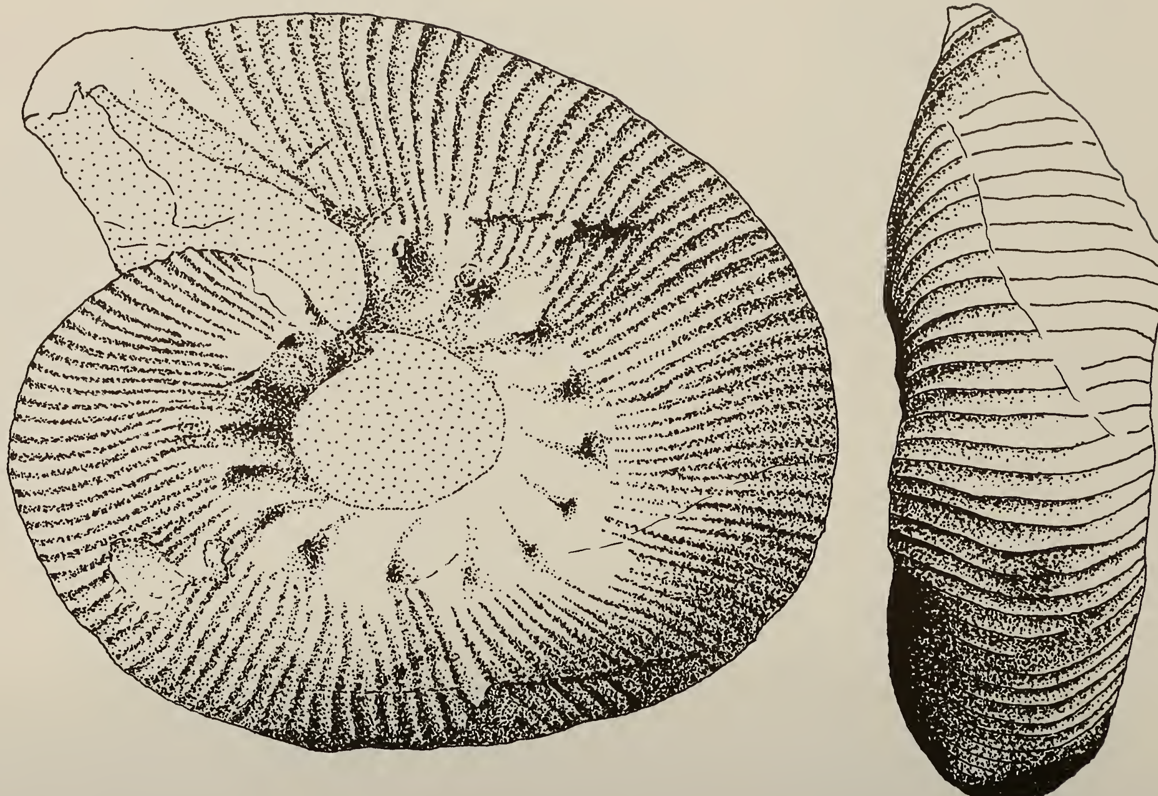

Fig. 168. *Olcostephanus* (*Olcostephanus*) *astieriformis* (Böse) (♀). The lectotype, designated herein, from the Taraises Formation of northern Mexico (after Böse 1923). × 1.

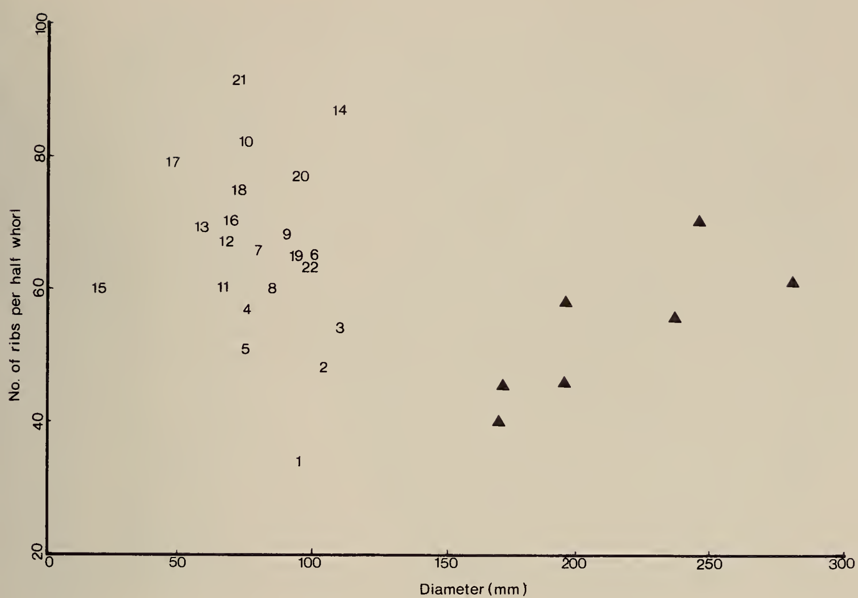

Fig. 169. Plot of rib density against diameter for 'species' of the *O. astierianus* plexus. Triangles represent individuals from the Sundays River Formation. 1 = *O. raricostatus* (Böse) (after Böse 1923, pl. 4 (fig. 1)), 2 = *O. quadriradiatus* Imlay (after Imlay 1938, pl. 5 (fig. 2)), 3 = *O. astieriformis* (Böse) (after Böse 1923, pl. 1 (fig. 2)), 4 = *O. scissus* (Baumberger) (after Baumberger 1907, fig. 107), 5 = *O. discoideus* Imlay (after Imlay 1938, pl. 2 (fig. 5)), 6 = *O. symonensis* (Böse) (after Böse 1923, pl. 2 (fig. 7)), 7 = *O. catulloi* (Rodighiero) (after Rodighiero 1919, pl. 9 (fig. 9)), 8 = *O. rabei* (Besairie) (after Besairie 1936, pl. 12 (fig. 8)), 9 = *O. astierianus* (d'Orbigny) (after Baumberger 1910, pl. 32 (fig. 1)), 10 = *O. sayni* (Kilian) (after Baumberger 1910, pl. 32 (figs 2–3)), 11 = *O. astierianus* (d'Orbigny) (*in* Baumberger 1910, pl. 29 (fig. 3)), 12 = *O. sayni* (SAM–9270), 13 = *O. scissus* (Baumberger) (*in* Baumberger 1907, pl. 23 (fig. 2)), 15 = *O. elongatus* (Tzankov) (after Tzankov 1943, pl. 6 (figs 3–4)), 16 = *O. scissus* (Baumberger) (*in* Matheron 1878, pl. B–20 (fig. 8)), 17 = *O. catulloi* (Rodighiero) (*in* Tzankov 1943, pl. 4 (figs 1–2)), 18 = *O. boesei* (Riedel) (after Riedel 1938, pl. 3 (fig. 1)), 19 = *O. astierianus* (d'Orbigny) (*in* Riedel 1938, pl. 3 (fig. 3)) 20 = *O. schafarziki* (Somogyi) (after Somogyi 1916, pl. 13 (fig. 3)), 21 = *O. filosus* (Baumberger) (*in* Bayle 1878, pl. 55 (fig. 2)), 22 = *O. astierianus* (d'Orbigny) (*in* Somogyi 1916, pl. 13 (fig. 2)).

Discussion

Amongst the collections from the Sundays River Formation are a rather large number of compressed macroconchs, unfortunately generally rather crushed and fragmentary. These forms differ from *O. uitenhagensis* in lacking the marked egression of the umbilical seam of the body chamber, and in that the tubercles remain bullate to the peristome.

These specimens are undoubtedly close to the type of the genus, *O. astierianus* (d'Orbigny) (Fig. 171). The latter species is rather compressed, with a moderately wide, deep, umbilicus and sloping umbilical walls ornamented with 16 radial primaries on the outer whorl. These terminate in prominent, somewhat

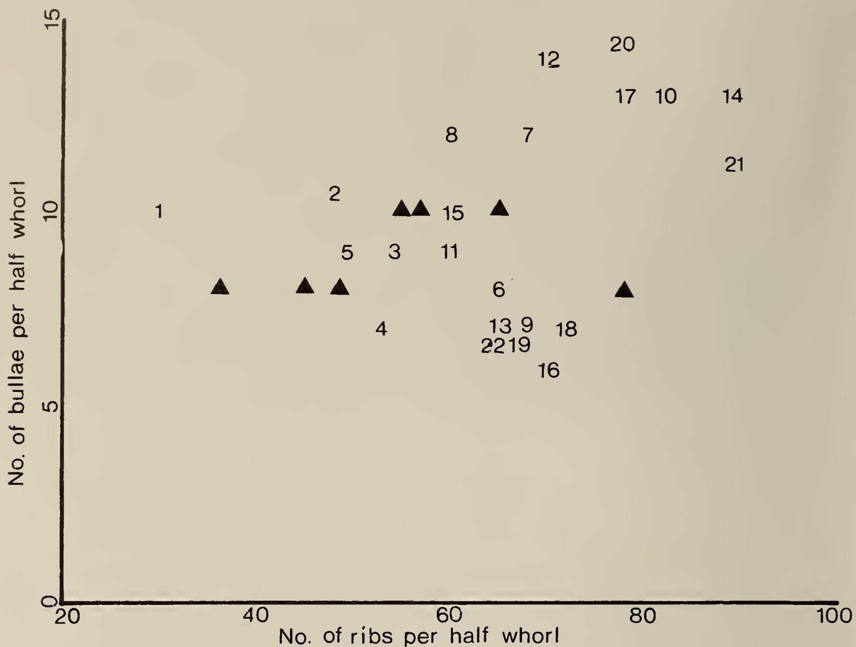

Fig. 170. Plot of rib density against umbilical bullae for 'species' of the *O. astierianus* plexus. Numbers and symbols as for Figure 85.

Fig. 171. *Olcostephanus astierianus* (d'Orbigny) (♀). Ventral and lateral views of the lectotype from the Lower Hauterivian of Castellane, France. × 1.

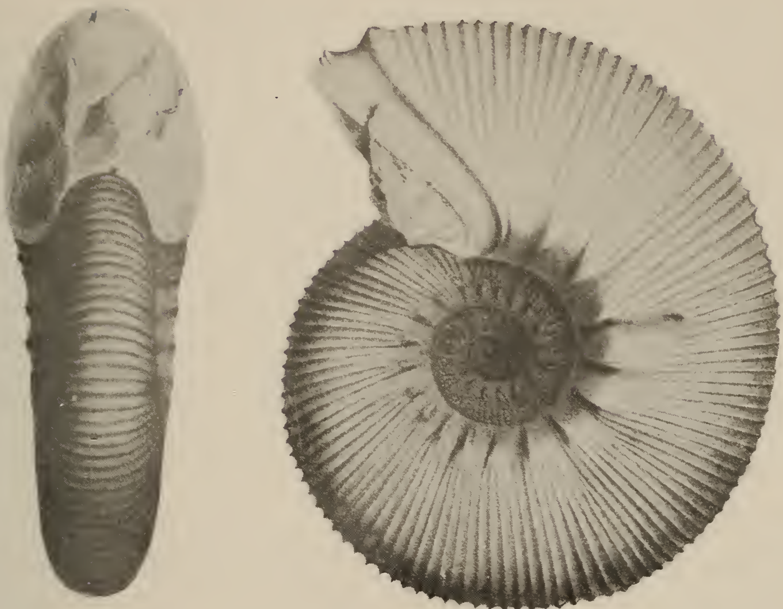

Fig. 172. *Olcostephanus* (*Olcostephanus*) *astierianus* (d'Orbigny) (♀). A copy of D'Orbigny's (1842*a*) protograph. × 1.

rounded umbilical tubercles on the outer whorl that give rise to bundles of 5–6, fine, prorsiradiate secondary ribs, commonly with 2–4 intercalatories between bundles. Contrary to D'Orbigny's (1840) (Fig. 172) protograph, the umbilical seam does not egress on the outer whorl, but remains just above the umbilical tubercles. This species seems to be based upon a macroconch, with a (?) simple peristome preserved at only 89 mm. According to Baumberger (1907: 28), the inner whorls bear parabolae, in which case they are to be expected on the outer whorls of the microconch. *Olcostephanus astierianus* differs from the present species in having fewer, rounded tubercles on the outer whorl and, perhaps, in possessing parabolae on the early whorls. Its small adult size, like much of the west European material, is probably environmentally controlled and is not herein considered of specific importance.

Olcostephanus astierianus globulosus (Kilian) (*in* Roch 1930: 313) was erected for the example of '*Astieria sayni*' figured by Baumberger (1908: 1, pl. 25 (fig. 3a–b)). Since, however, the specimen in question is listed as '*Astieria guebhardi*', presumably it is this individual to which Kilian referred. In the writer's opinion, it is too inflated and with too many bullate umbilical tubercles to be conspecific with *O. astierianus*. Indeed, the original identification, that is as *O. guebhardi*, is more likely to be correct.

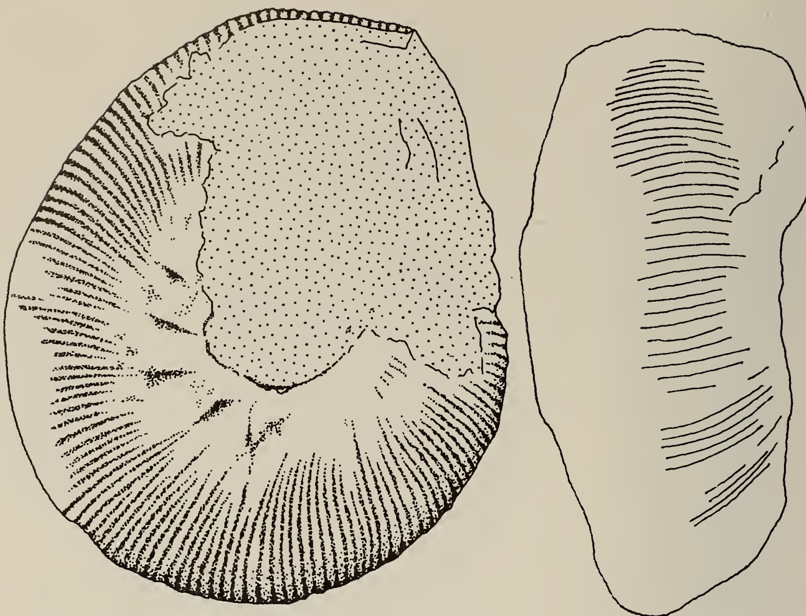

Fig. 173. *Olcostephanus* (*Olcostephanus*) *boesei* (Riedel). The holotype from the Upper Valanginian of Caqueza, Colombia (after Riedel 1938). × 1.

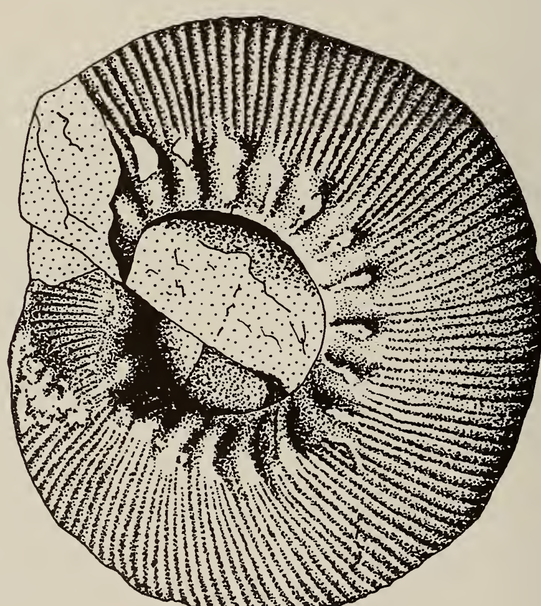

Fig. 174. *Olcostephanus* (*Olcostephanus*) *catulloi* (Rodighiero). The holotype from Venice (after Rodighiero 1919). × 1.

Olcostephanus boesei (Riedel) (Fig. 173) is a somewhat compressed species with a moderately wide umbilicus and steep umbilical walls. The latter are ornamented with 7–8 relatively pronounced primary ribs per half whorl, each terminating in a bulla on the umbilical shoulder and giving rise to 4–5 fine, prorsiradiate secondaries. There is commonly 3–4 intercalated ribs between bundles. Parabolae seem to be lacking. This is a finely ribbed species of the *astierianus* plexus which was compared with *O. sayni* (Kilian), from which it was distinguished by its fewer umbilical bullae. It is, therefore, doubtfully separable from *O. scissus* (Baumberger).

Olcostephanus catulloi (Rodighiero) (Fig. 174) is a moderately involute species with a fairly narrow umbilicus. About 25 primary ribs on the outer whorl terminate in prominent bullae on the umbilical shoulder, from which arise 3–5 prorsiradiate secondaries with 1–3 intercalated ribs between bundles. There are 16 secondaries per 3 bullae, with about 125 ribs across the venter of the outer whorl. This species differs from *O. astieriformis* in being more finely and densely ribbed, with more numerous umbilical bullae. It is, therefore, close to *O. sayni*.

Olcostephanus destefanii (Rodighiero, 1919) is a finely ribbed species, allied to *O. sayni*, which is yet to be figured. Between 14 and 15 primary ribs terminate in tubercles on the umbilical shoulder and give rise to bundles of fine, slightly flexuous secondaries, with intercalated ribs between bundles. It differs from *O. astieriformis* in its finer, denser, flexuous secondary ribbing, in which respect it approaches *O. sayni gerecseiensis* Somogyi.

Fig. 175. *Olcostephanus* (*Olcostephanus*) *elongatus* (Tzankov). The holotype from the Upper Valanginian of Placovo, Bulgaria (after Tzankov 1943). × 4.

Fig. 176. *Olcostephanus* (*Olcostephanus*) *filosus* (Baumberger) (♀). The lectotype, designated herein, from the Swiss Jura (after Baumberger 1907). × 1.

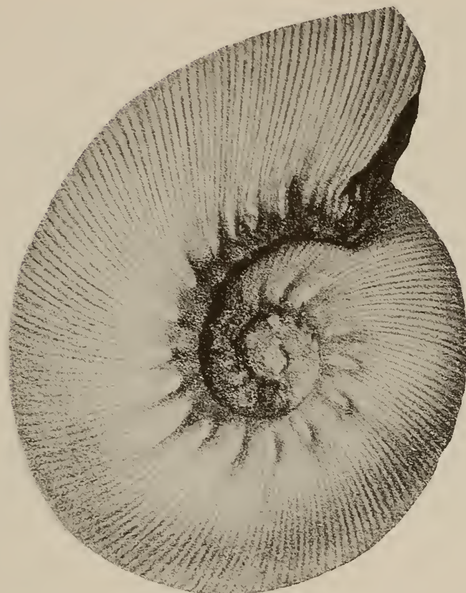

Fig. 177. *Olcostephanus* (*Olcostephanus*) *filosus* (Baumberger) (after Bayle 1878), × 1.

Olcostephanus elongatus (Tzankov) (Fig. 175) is based upon a strongly compressed, crushed juvenile only 20 mm in diameter. There are about 20 primaries on the outer whorl which terminate in bullae on the umbilical shoulder, from which arise 4–5 prorsiradiate secondaries, some of which occasionally bifurcate. Parabolae are lacking and the outer whorl shows a rapid increase in height (? due to crushing). This species is close to *O. astieriformis* but seems to be more densely ribbed and is thus doubtfully separable from *O. symonensis* (Böse).

Olcostephanus filosus (Baumberger) (Fig. 176) is a rather compressed macroconch species with a moderately wide umbilicus and steep umbilical walls. About 26 slightly rursiradiate primary ribs terminate in bullae on the umbilical shoulder and give rise to bundles of 9–10, very fine, prorsiradiate secondaries between which are fine intercalatories. Parabolae apparently lacking. This species is readily distinguishable from *O. astieriformis* by its much denser, finer ribbing. Although *O. filosus* has somewhat more primary ribs than *O. sayni*, individuals such as that figured by Bayle (1878) (Fig. 177 herein) suggest that this character is somewhat variable and population studies are likely to show that *O. filosus* is a junior subjective synonym of *O. sayni*. Unfortunately the concept of *O. filosus* has become somewhat confused by the inclusion of the specimen figured by Matheron (1878) as *Ammonites mittreanus* [*sic*] d'Orbigny into Baumberger's (1907) species. Matheron's (1878) example (Fig. 178) is

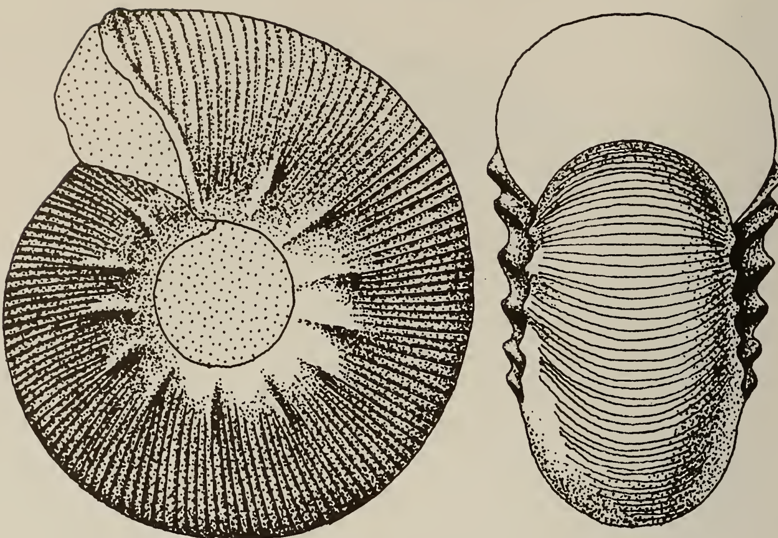

Fig. 178. *Olcostephanus* (*Olcostephanus*) *scissus* (Baumberger). Matheron's oft-quoted figure of *O. mittreanus* d'Orbigny, based on a specimen from the south of France, and assigned by most authors to *O. filosus* (Baumberger) (after Matheron 1878). × 1.

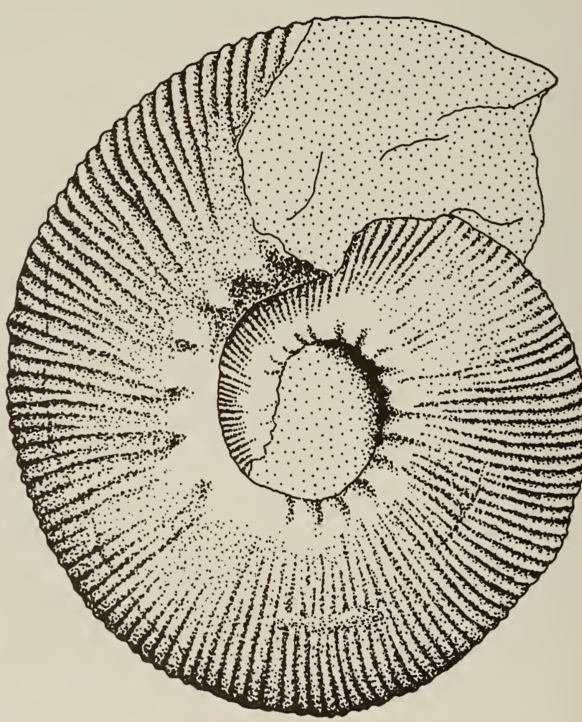

Fig. 179. *Olcostephanus* (*Olcostephanus*) *paronae* (Rodighiero). The holotype, by monotypy, from Venice (after Rodighiero 1919). × 1.

easily distinguished, from both *O. sayni* and *O. filosus*, in the presence of only 14 umbilical bullae on the outer whorl. This individual should, therefore, be assigned to *O. scissus* (Baumberger).

Olcostephanus paronae (Rodighiero) (Fig. 179) is another species which is closely allied to *O. sayni*. It shows marked egression of the umbilical seam on the outer (?final) whorl so that about 40 per cent of the preceding whorl is visible in the umbilicus. The umbilical wall is steep on the inner whorls. The final whorl is ornamented with about 20 umbilical tubercles from which arise bundles of 3–4 prorsiradiate secondary ribs which frequently bifurcate. On the adoral half of the outer whorl (?the body chamber), nearly every long rib bifurcates and has an adjacent intercalated rib high up on the flank. The finer, denser secondaries, and their frequent bifurcation, distinguish this species from *O. astieriformis*.

Olcostephanus potosinus Castillo & Aguilera (Fig. 180) was based upon two individuals, without type designation. Consequently, the original of the specimen here figured is selected as lectotype. This specimen is a strongly compressed, crushed, individual which shows frequent umbilical bullae from which arise 3–6 prorsiradiate secondaries so that there are about 120–130 secondary ribs across the venter of the lectotype. This species is close to *O. astieriformis* but seems to be more finely ribbed and, as such, probably has priority over *O. symonensis* (Böse) from the same region.

Olcostephanus quadriradiatus Imlay (Fig. 181) has an ovate, compressed whorl section with a moderately narrow umbilicus and vertical umbilical walls. Primary ribs terminate in 23 prominent umbilical bullae on the outer whorl from which arise bundles of 3–5 slightly prorsiradiate, almost radial secondaries with 1–2 intercalated ribs between bundles. This is a macroconch species in which parabolae are apparently lacking. This species differs from *O. astieriformis* only in the almost radial direction of its secondary ribs. Population studies may show that this character is not of specific importance.

Olcostephanus raricostatus (Böse) (Fig. 182) is a compressed species with a narrow umbilicus and arched venter. Rursiradiate primaries terminate in 18–23 bullae on the umbilical shoulder, from which arise 3–4 slightly flexuous, prorsiradiate secondary ribs which frequently bifurcate. Parabolae are apparently lacking. The distant ribbing of this species is distinctive and it seems likely that *O. huizachensis* (Cantu Chapa) is based upon either the microconch or the inner whorls of the macroconch of *O. raricostatus*.

Olcostephanus sayni (Kilian) (Fig. 183) is a compressed species with a moderately narrow umbilicus and a subtrigonal whorl section. The umbilical seam of the lectotype egresses markedly on the outer whorl, suggesting this is also the final whorl. The steep umbilical walls are ornamented with about 22 radial primaries which terminate in bullae on the umbilical shoulder and give rise to bundles of 4–5, fine, prorsiradiate secondaries which frequently bifurcate. There are 1–2 intercalated ribs between bundles. On the adoral portion of the outer whorl of the lectotype there are 23 ribs across the venter per 4 umbilical

Fig. 180. *Olcostephanus* (*Olcostephanus*) *potosinus* Castillo & Aguilera (♀). The lectotyde, designated herein, from northern Mexico (after Castillo & Aquilera 1895). × 1.

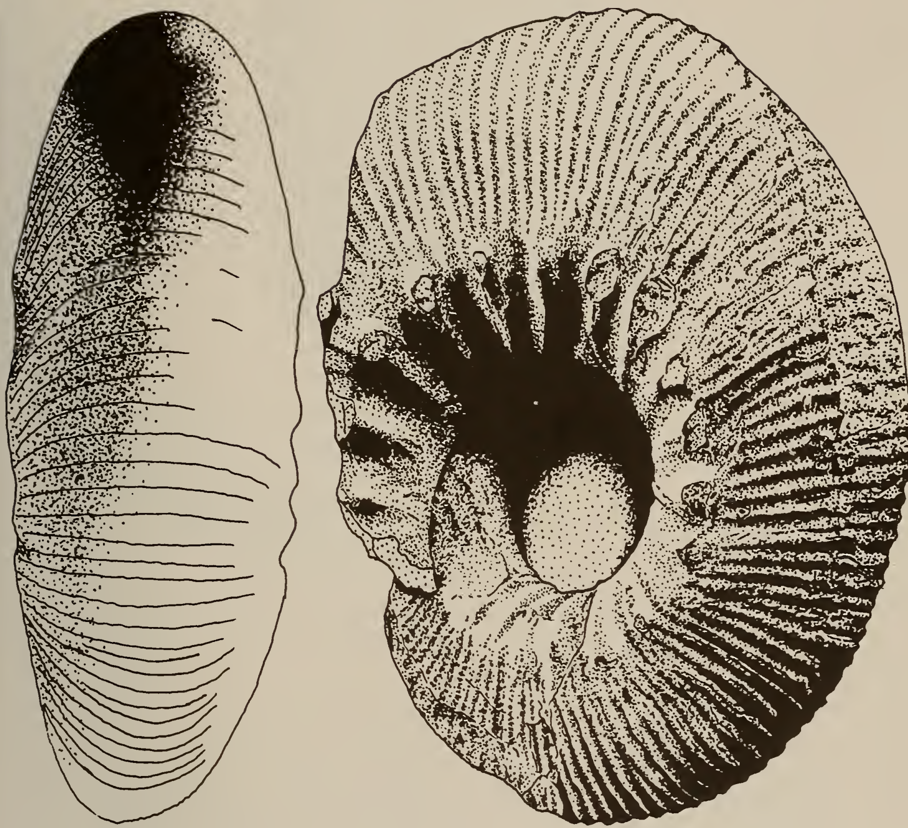

Fig. 181. *Olcostephanus* (*Olcostephanus*) *quadriradiatus* Imlay (♀). The holotype from the Taraises Formation of northern Mexico (after Imlay 1938). × 1.

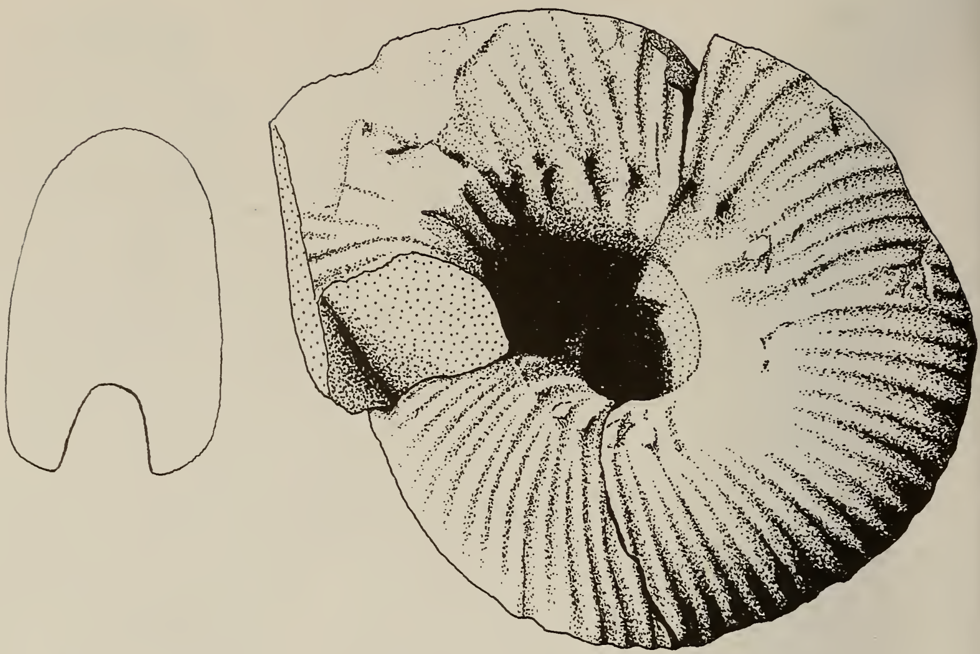

Fig. 182. *Olcostephanus* (*Olcostephanus*) *raricostatus* (Böse) (♀). The lectotype, designated herein, from the Taraises Formation of northern Mexico (after Böse 1923). × 1.

Fig. 183. *Olcostephanus* (*Olcostephanus*) *sayni* (Kilian). The lectotype from the Lower Hauterivian of Castellane, France × 1.

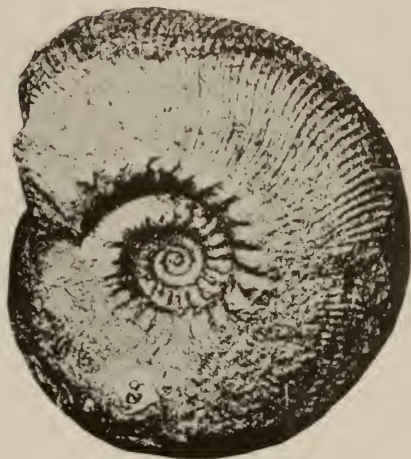

Fig. 184. *Olcostephanus* (*Olcostephanus*) *sayni gerecseiensis* (Somogyi). The holotype (after Somogyi 1916). × 1.

bullae. Parabolae are lacking. This species may be distinguished from the present material by its more numerous umbilical bullae and finer, denser secondary ribs. Somogyi (1916) distinguished *O. sayni gerecseiensis* (Fig. 184) on the basis of its flexuous secondary ribbing.

Olcostephanus scissus (Baumberger) (Fig. 185) is a species which has long been confused with *O. filosus* and *O. sayni*, from which it is readily distinguishable by its fewer umbilical bullae. It is a compressed form with a narrow umbilicus and sloping umbilical walls ornamented with 14 radial primaries. These terminate in bullae giving rise to generally 4, fine, prorsiradiate secondaries which frequently bifurcate high up on the flank. There are frequent intercalated ribs between bundles and parabolae are apparently lacking. This species is very close to *O. astierianus* from which it seems to differ only in possessing bullate umbilical tubercles and in the frequent bifurcation of the secondary ribs in *O. scissus*. *O. astieriformis* has more numerous bullae and does not show bifurcation of the secondary ribs.

Olcostephanus subfilosus Spath (Fig. 186) is based upon a nucleus which bears parabolae and displays about 16 umbilical bullae from which arise numerous fine, prorsiradiate secondaries, with intercalated ribs between bundles. A topotype example (Fig. 187) in the Oxford University Museum, OUM–K1207, shows a rather narrow, deep, crater-like umbilicus with steep, convex walls and an evenly rounded umbilical shoulder. Primary ribs begin at, or close to, the umbilical seam and curve backwards (rursiradiate) to about 20 bullae on the umbilical shoulder of the outer whorl. Each bulla gives rise to 4–6 prorsiradiate secondaries with 1–2 intercalated ribs between bundles. There are about 125 ribs on the outer whorl. The flanks are convex, converging towards the narrowly arched venter and giving the whorl section a subtrigonal outline.

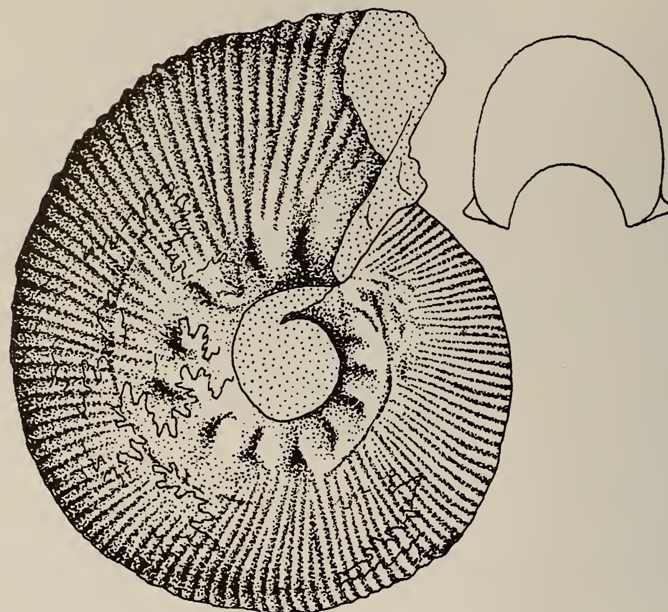

Fig. 185. *Olcostephanus* (*Olcostephanus*) *scissus* (*Baumberger*). The holotype, by lectotype designation herein, from the Swiss Jura (after Baumberger 1907). × 1.

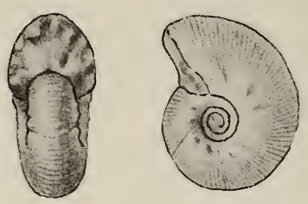

Fig. 186. *Olcostephanus* (*Olcostephanus*) *subfilosus* Spath. The holotype from Speeton, Yorkshire (after Pavlow & Lamplugh 1892). × 0,5.

There are two distinct, oblique parabolae on the outer whorl. This species seems to be based upon a juvenile of *O. sayni*, although the presence of parabolae have still to be proven on the inner whorls of the latter species.

Olcostephanus symonensis (Böse) (Fig. 188) was distinguished from *O. astieriformis* by its finer, more numerous secondaries with 60 in a space where *O. astieriformis* shows only 45. It is, therefore, close to *O. potosinus*, as well as resembling *O. sayni* in the frequent bifurcation of secondary ribs. With revision, it seems likely that Böse's (1923) species will fall into synonymy.

There is in the Natural History Museum in Paris a cast of the original of Paquier's (1900) *Holcostephanus variegatus* (Fig. 189). It shows the original to

Fig. 187. *Olcostephanus* (*Olcostephanus*) *subfilosus* Spath. A topotype example in the Oxford University Museum. Note the subtrigonal whorl section, numerous bullae and parabolae. This species may be based on the inner whorls of *O. sayni* (Kilian). × 2.

be poorly preserved and abraded, so much so that it is difficult to discern many of the umbilical bullae and ribs on the outer whorl and these could not be counted. What can be seen of the ribbing shows rather fine secondaries, about as wide as the interspaces, which frequently bifurcate on the flanks. There is a prominent parabola near the adoral end of the outer whorl, which displays a subtrigonal whorl section. This species is close to *O. sayni* but with distinctly coarser ribbing. It can be distinguished from *O. scissus* and *O. astieriformis* by the presence of parabolae.

Occurrence

This species is currently known only from northern Mexico and South Africa.

Olcostephanus (*Olcostephanus*) *coahuilensis* Imlay, 1938 (♀)

Figs 190A–B, 191

Olcostephanus coahuilensis Imlay, 1938: 553, pl. 1 (figs 1–3).

Material

A single macroconch, SAM–PCU1550, retaining recrystallized test.

Holotype

The original of *Olcostephanus coahuilensis* Imlay (Fig. 191) from the Taraises Formation of northern Mexico.

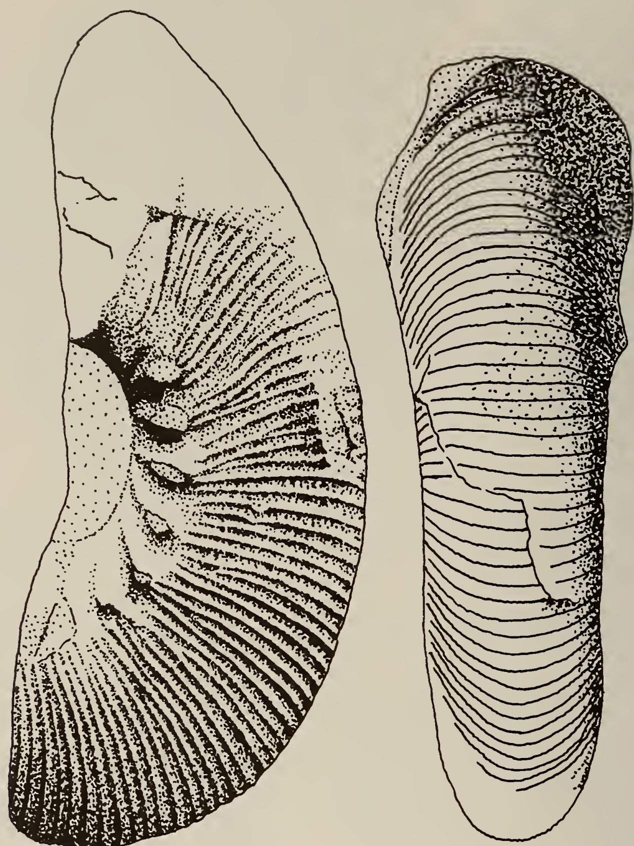

Fig. 188. *Olcostephanus* (*Olcostephanus*) *symonensis* (Böse) (♀). The lectotype, designated herein, from the Taraises Formation of northern Mexico (after Böse 1923). × 1.

Fig. 189. *Olcostephanus* (*Olcostephanus*) *variegatus* (Paquier). A cast of the holotype in the Natural History Museum, Paris. × 1.

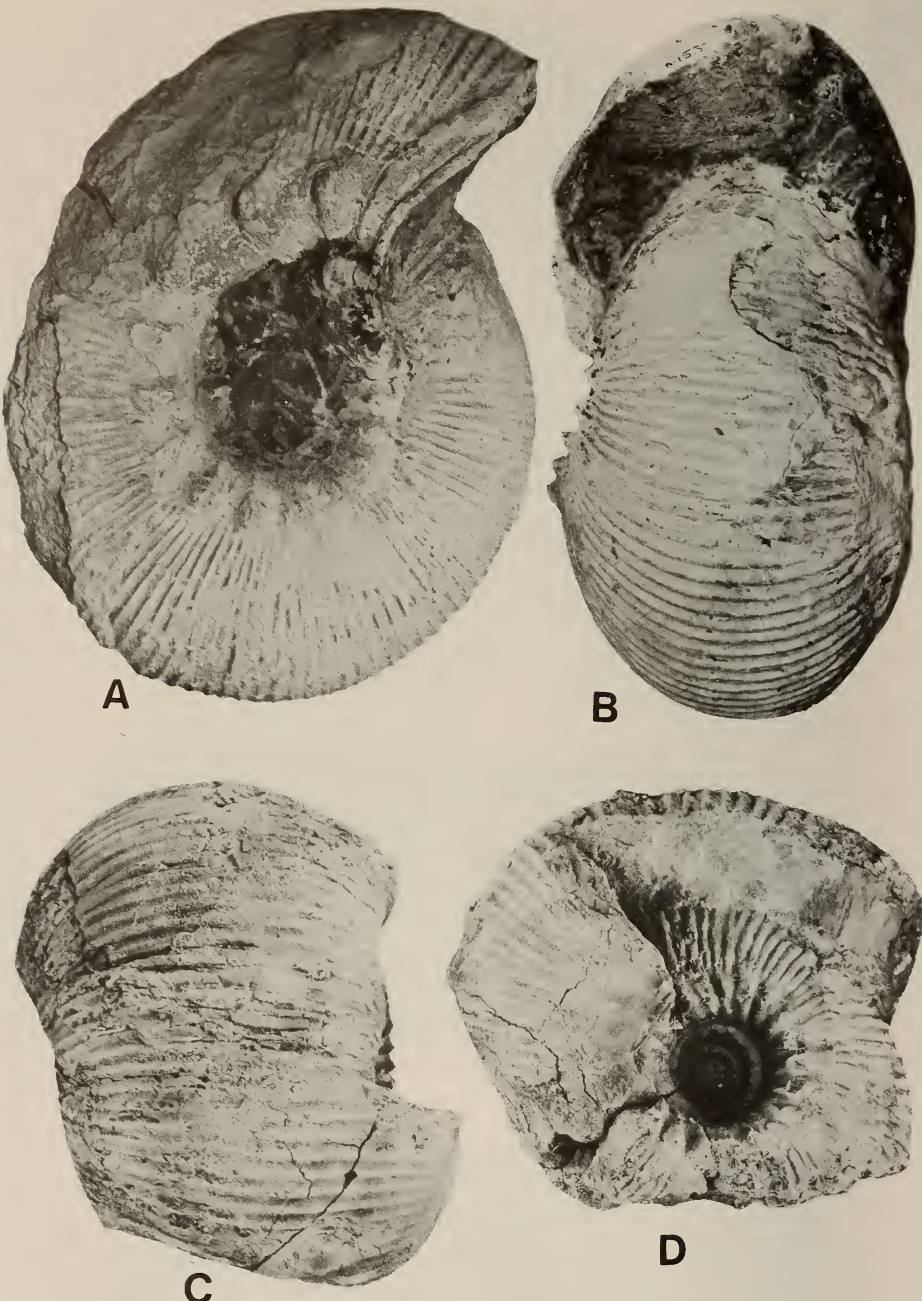

Fig. 190. A–B. *Olcostephanus* (*Olcostephanus*) *coahuilensis* Imlay (♀). Lateral and front views of SAM–PCU1550, showing moderate inflation and fine, radial secondaries. × 0,44. C–D. *Olcostephanus* (*Olcostephanus*) cf. *perinflatus* (Matheron) (♀). Ventral and lateral views of AM–4292b. Note small umbilicus, extreme inflation, fine secondaries occasionally bifurcating, and apparent absence of parabolae. × 0,75.

Description

The shell is a large, inflated cadicone, involute up to the umbilical bullae, except on the final whorl when the umbilical seam egresses somewhat. The umbilicus is narrow with moderately steep, convex umbilical walls, the latter ornamented with 17 rursiradiate primaries which terminate in bullae on the umbilical shoulder. From these arise 4–5 radial secondaries, commonly with 1–2 intercalatories between bundles. There are 32 secondaries per 5 bullae on the outer whorl, with 11 ribs in a 50 mm distance along the venter, and about 50 ribs per half whorl. Maximum inflation is attained about half a whorl behind the peristome.

Measurements

No.	D	H	Wi	W/H	Uo	Ui
SAM–PCU1550	195	75	90	1,20	87	52 (27)

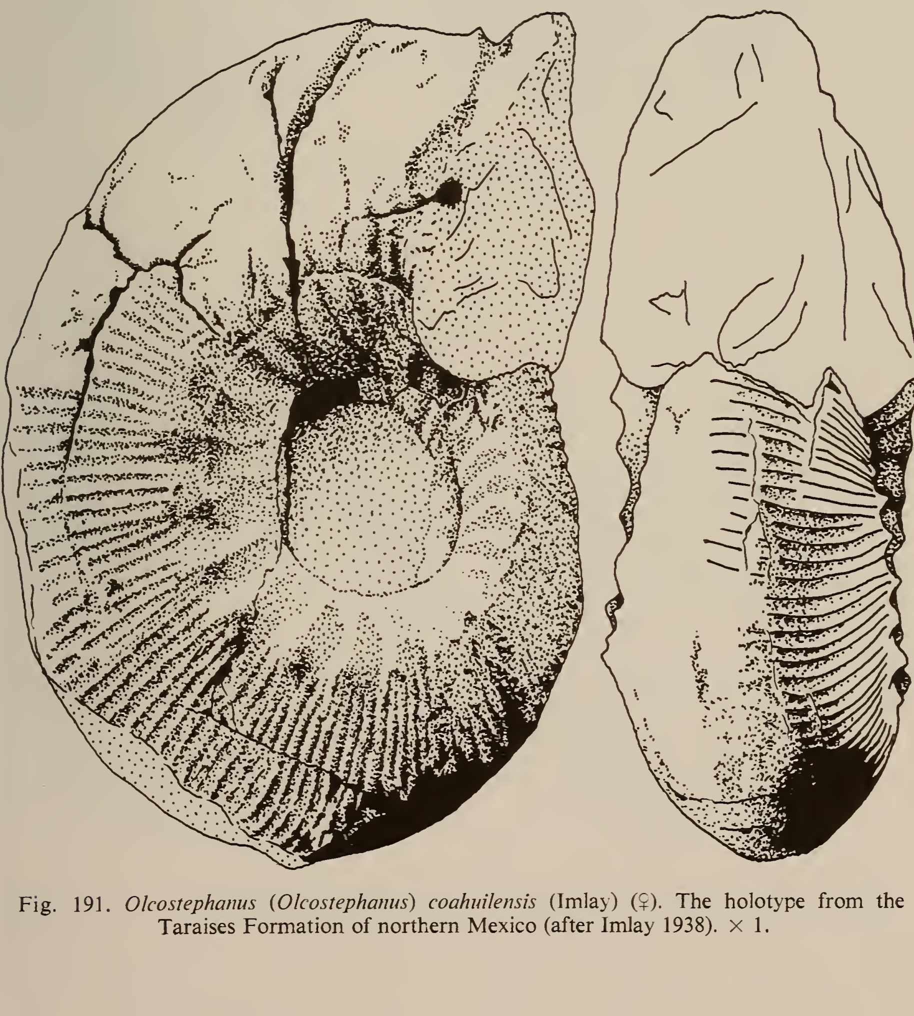

Fig. 191. *Olcostephanus* (*Olcostephanus*) *coahuilensis* (Imlay) (♀). The holotype from the Taraises Formation of northern Mexico (after Imlay 1938). × 1.

Fig. 192. *Olcostephanus* (*Olcostephanus*) *guebhardi* (Kilian). The holotype from Escragnolles, France (after Kilian 1902). × 1.

Discussion

The Uitenhage example differs from Imlay's type only in having slightly fewer umbilical bullae per whorl, a difference which is not considered of specific importance.

Olcostephanus guebhardi (Kilian) (Fig. 192), of which *O. sharpei* (Karakasch) (Fig. 193) is a synonym, closely resembles the South African material, but is much smaller and does not show the inflation seen in the present shell The differences may well be those between dimorphs, but until the European material is revised, the writer prefers to use Imlay's name. *Olcostephanus actinotus* (Baumberger) also resembles the present species, but has a very different, subtrigonal whorl section.

Occurrence

Olcostephanus coahuilensis is currently known only from Mexico and South Africa.

Olcostephanus (*Olcostephanus*) cf. *perinflatus* (Matheron, 1878) (♀)

Figs 151E–F, 190C–D, 194–195

Compare

Ammonites perinflatus Matheron, 1878: pl. 20B (fig. 8a–b).
Ammonites stephanophorus Matheron, 1878: pl. 20B (fig. 9).

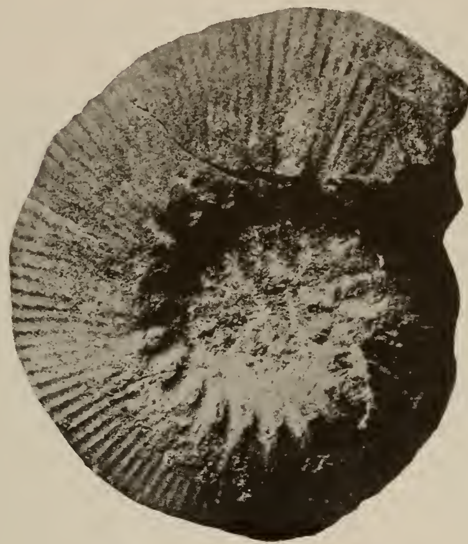

Fig. 193. *Olcostephanus* (*Olcostephanus*) *guebhardi* (Kilian). The holotype of *Astieria sharpei* Karakasch from the Upper Valanginian of the Crimea (after Karakasch 1907). × 1.

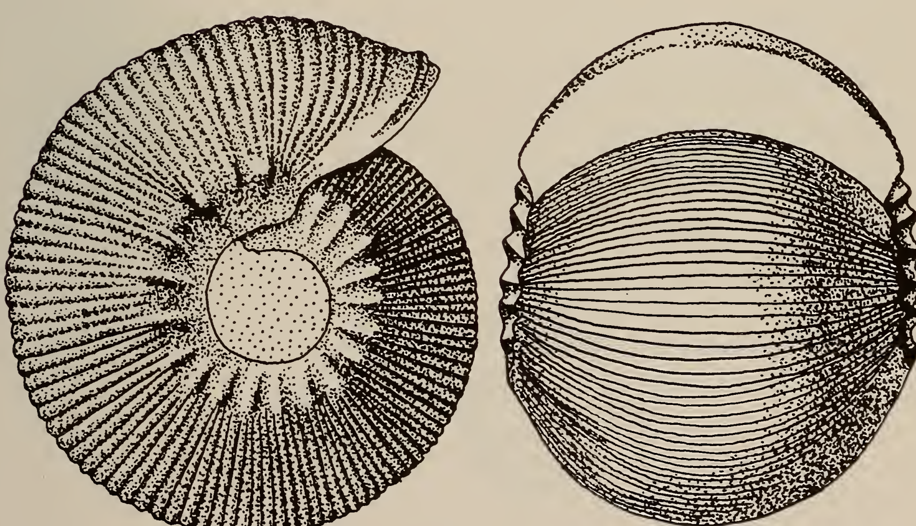

Fig. 194. *Olcostephanus* (*Olcostephanus*) *perinflatus* (Matheron) (♀). The holotype, by monotypy, from the south of France (after Matheron 1878). × 1.

Olcostephanus perinflatus (Matheron) Spath, 1939: 23. Fatmi, 1977: 270.
Olcostephanus cf. *perinflatus* (Matheron) Spath, 1939: 25, pl. 6 (fig. 6).

Material

Two specimens, AM–4292b, and PEM–1468/89, the latter a mere fragment, both preserved as internal moulds.

Holotype

The original of Matheron's (1878) plate 20B (fig. 8a–b) (Fig. 194 herein) from the south of France.

Description

The shell of AM–4292b is an extremely inflated, globose, cadicone, with a very narrow, deep, crater-like umbilicus. The umbilical walls are steep, convex, and slightly overhanging, and ornamented with about 22 rursiradiate primaries terminating in small bullae on the umbilical shoulder. The latter give rise to 3–4 rather fine, slightly prorsiradiate secondaries, which on the outer whorl are slightly flexuous, and between which are generally a single intercalated rib. Very occasionally a secondary rib is seen to bifurcate on the flanks, so that there are about 50–60 secondaries per half whorl on the outer whorl. Parabolae are absent on the outer whorl, but it is unknown whether they occur on the inner whorls.

Discussion

As suggested by Kilian (1892), the writer believes *Ammonites stephanophorus* Matheron (Fig. 195) merely to represent the juvenile growth stages of *Olcostephanus perinflatus*. The Uitenhage specimens are only tentatively referred to Matheron's species because of uncertainty as to what *O. perinflatus* really looks like, since it has never been photographically refigured or redescribed and there is reason to believe that Matheron's (1878) illustration may be somewhat idealized.

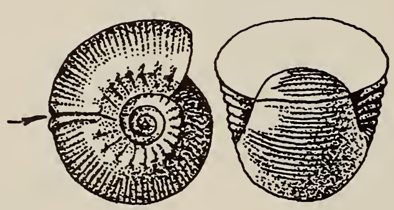

Fig. 195. *Olcostephanus* (*Olcostephanus*) *perinflatus* (Matheron) (♀). The holotype of *Olcostephanus stephanophorus* (Matheron) from the south of France, a juvenile (after Matheron 1878). × 1.

Fig. 196. *Olcostephanus* (*Olcostephanus*) *balkanicus* (Tzankov). The syntypes from the Lower Hauterivian of Bulgaria (after Tzankov 1943). × 3.

Olcostephanus globosus Spath, of which *O. pachycyclus* Spath represents an early growth stage (Fatmi 1977), is a macroconch species which is undoubtedly close to *O. perinflatus*. Indeed, it would seem to differ from Matheron's (1878) illustration only in its larger adult size, a character which is possibly environmentally related and hence doubtfully of specific importance. However, the Pakistan material is retained as distinct until Matheron's (1878) species is restudied on the basis of type and topotype material.

Olcostephanus balkanicus (Tzankov) (Fig. 196) is based upon a strongly inflated nucleus which seems to differ from the inner whorls of *O. perinflatus*, that is from *O. stephanophorus*, in having a much wider umbilicus, somewhat fewer (15–17) umbilical bullae and distinctly prorsiradiate secondaries. However, it shows prominent parabolae.

Occurrence

Olcostephanus perinflatus is at present known with certainty only from the south of France, but it may also be present in South Africa and Pakistan.

Family **Berriasellidae** Spath, 1922

Subfamily Neocomitinae Spath, 1924

Genus *Neohoploceras* Spath, 1939

Type species *Ammonites submartini* Mallada, 1882;
by original designation of Spath, 1939

Neohoploceras subanceps (Tate, 1867)

Fig. 197

Ammonites subanceps Tate, 1867: 150, pl. 7 (fig. 3a–b).
Reineckia subanceps (Tate) Newton, 1896: 150.
? *Leopoldia depereti* Sayn, 1907: 59, pl. 4 (figs 6–7).
Solgeria subanceps (Tate) Spath, 1930: 151, pl. 13 (fig. 4a–c). Du Toit, 1954: 384.
Neohoploceras subanceps (Tate) Klinger & Kennedy, 1979: 18.

Material

The holotype, BM–C32197, from the Sundays River is the only undoubted specimen known.

Holotype

By monotypy, the original of *Ammonites subanceps* figured by Tate (1867: 150, pl. 7 (fig. 3a–b)), from the Sundays River, and now in the British Museum, BM–C32197.

Fig. 197. *Neohoploceras subanceps* (Tate). The holotype, BMNH–C32197, from the Sundays River Formation. × 2. Photo: W. J. Kennedy.

Diagnosis

Small, somewhat inflated, with 12–14 ribs beginning at the umbilical seam of the outer whorl, each rib with a weak umbilical bulla and terminating in a swollen tubercle at about mid-flank, from which prorsiradiate ribs bifurcate or trifurcate. There are occasional single and intercalated ribs. All ribs terminate in small ventrolateral tubercles and are interrupted across the venter by a smooth zone. Constrictions are present.

Description

The following description is based on a plastercast of the type sent to the writer by M. K. Howarth: the specimen is small, but appears to have recrystallized test preserved. The shell is somewhat compressed, with a whorl section about as wide as high. The umbilicus is rather shallow and moderately evolute, the outer whorl covering slightly more than half of the preceding whorl. Maximum width is at mid-flank. The umbilical wall is gently sloping, with a well-rounded umbilical shoulder.

On the outer whorl, about 12–14 ribs begin at the umbilical seam and pass almost radially outwards to the umbilical shoulder where they develop small but distinct umbilical bullae. From here the ribbing is slightly prorsiradiate, and commonly swells at about mid-flank into a lateral tubercle, from which ribs frequently bifurcate or trifurcate. Occasionally only a single rib arises from the mid-lateral tubercle, in which case the latter is usually weakly developed, while there is also the odd intercalated rib. Ribbing is very weakly developed across the venter on the adoral portion of the outer whorl, and gives the impression that the smooth zone may have disappeared with age. There appear to be two constrictions on the outer whorl.

Measurements

No.	D	H	Wi	W/H	Uo	Ui
BM–C32197	16	8	7,5	0,94	7	5 (31)

Discussion

The small size of the holotype, which represents a juvenile growth stage, does not allow for proper comparison with other species, especially since juveniles are rarely figured or described. One of the few exceptions is the work of G. Sayn (1907). Amongst the examples figured by Sayn, *N. depereti* and *N. provinciale* (Sayn) both bear a close resemblance to *Ammonites subanceps.*

Neohoploceras depereti (Sayn) is moderately inflated and bears prominent constrictions. The ribbing is of two types, simple ribs lacking tubercles and stronger ribs which bifurcate or trifurcate from a prominent lateral tubercle and also have umbilical tubercles. All ribs bear weak ventrolateral clavi. The venter is grooved and smooth. The only difference between *N. depereti* and *N. subanceps* appears to be in the possession of more prominent tubercles by the former. However, since the larger of Sayn's syntypes is 33 mm in diameter, as against only 20 mm for *N. subanceps*, the differences are probably only ontogenetic.

Neohoploceras provinciale (Sayn) is similar to *N. subanceps* but is even larger than *N. depereti* and consequently comparison is still more difficult. It is, however, more closely ribbed than *N. depereti*, although its validity will be resolved only with a revision of the French material.

It is not possible to compare satisfactorily the South African species with

the rich Madagascan faunas due to the size differences. Such a comparison will have to await ontogenetic studies on the Madagascan material.

Occurrence

Neohoploceras subanceps is present in the Sundays River Formation and perhaps the zone of *Saynoceras verrucosum* in south-east France.

Genus *Distoloceras* Hyatt, 1900

Type species *Ammonites hystrix* Phillips, 1829;
by original designation of Hyatt, 1900

Distoloceras spinosissimum (Hausmann, 1837)

Figs 198–200

Ammonites spinosissimum Hausmann, 1837: 1458.
Crioceras spinosissimum (Hausmann) Holub & Neumayr, 1882: 273, pl. 1 (fig. 1a–c). Kitchin, 1908: 225.
? *Distoloceras* cf. *spinosissimum* (Hausmann) Spath, 1924: 75.
Distoloceras spinosissimum (Hausmann) Spath, 1930: 152, pl. 13 (fig. 1). Besairie, 1932: 44, pl. 16 (fig. 13). Du Toit, 1954: 384. Collignon, 1962: 51, fig. 887.
Distoloceras hirtzi Collignon, 1962: 32, pl. 185 (figs 846–849).

Material

The holotype, in the Greifswalde Universitäts-Museum, and two examples in the British Museum (BM–C32194, C10819) are the only specimens so far recorded from the Sundays River Formation.

Holotype

By monotypy, the original of *Crioceras spinosissimum* (Hausmann) figured by Holub & Neumayr (1882: 273, pl. 1 (fig. 1a–c)) from the Sundays River.

Diagnosis

Only uncoiled fragments of this species are known from the Uitenhage Group. At this stage the whorl section is polygonal, slightly compressed, with flat flanks. Ornament comprises strong radial ribs ornamented with umbilical, lateral and ventrolateral tubercles, between which are intercalated varying numbers of weaker, more flexuous ribs which may or may not have lateral and ventrolateral tubercles. The umbilical and ventrolateral tubercles frequently form spines. Ribbing joining the ventrolateral spines across the venter is convex adorally.

Description

This is a large species of *Distoloceras* of which only uncoiled fragments are currently known from the Sundays River Formation.

In the holotype, judging from Holub & Neumayr's figure, the adapical

Fig. 198. *Distoloceras spinosissimum* (Hausmann). The holotype from the Sundays River Formation (after Holub & Neumayr 1882). × 0,75.

portion of the outer whorl, which has already lost contact with the previous whorl, shows simple straight, uniformly developed radial ribbing, with umbilical and lower ventrolateral swellings (corresponding to the lateral tubercles on the adoral portion), although Spath (1930: 152) thought this was possibly due to corrosion.

Beyond a diameter of about 100 mm intercalated ribs start appearing, always lacking umbilical tubercles, but occasionally with swelling corresponding to the lateral tubercles. These intercalatories commonly arise at the umbilical shoulder, although some may be intercalated half-way up the flank, and vary considerably in strength.

With the appearance of intercalated ribs, the ventrolateral and umbilical tubercles frequently form long spines. These ventrolateral spines may also be developed on intercalated ribs.

Ribbing weakens somewhat across the tabulate venter and is convex adorally. The suture line is complex.

A cast of the specimen figured by Spath (1930: pl. 13 (fig. 1)) (BM–C32194), provided by M. K. Howarth, shows the following features:

Whorl compressed, polygonal in costal section, elliptical intercostally. Dorsum with a weak median furrow, from which at least some of the ribs arise and pass backwards (rursiradiate) to the dorsal (umbilical) shoulder. On the adapical portion of this uncoiled fragment, the flank ribs are very slightly prorsiradiate. Some are more prominent than others and show faint umbilical bullae, midlateral, and ventrolateral tubercles. Between these prominent ribs are intercalated finer ribs which arise above the level of the dorsal shoulder and show weak midlateral bullae and ventrolateral swellings. All ribs bend sharply forwards at the level of the midlateral tubercles. On the adoral portion of this specimen the main ribs all possess well-developed umbilical, midlateral, and ventrolateral spines, and are separated by 3–4 much finer, slightly flexuous ribs with small midlateral bullae and ventrolateral swellings. The ribbing is poorly developed across the venter.

Discussion

In describing a fragment of a tightly coiled form from the Upper Valanginian of Ambiky, Madagascar, Collignon (1962) considered this species to be characterized by '. . . section subcarrée, ornamentation de côtes à tubercles ou les externes acquierent la preponderance'.

Comparison of *D. spinosissimum* with coiled species of *Distoloceras* is most unsatisfactory and consequently the validity of this species will have to await the further collection of topotype material. It should be noted, however, that both Besairie (1932) and Collignon (1962) consider fragments of this species, which occurs plentifully in Madagascar, to be easily recognizable and typical.

Distoloceras hystrix (Phillips) would seem to be very similar, but with a more compressed whorl section (although it seems highly likely that the whorl

Fig. 199. *Distoloceras spinosissimum* (Hausmann). Ventral and lateral views of BMNH–C32194, figured by Spath (1930). × 0,66. Photo: W. J. Kennedy.

Fig. 200. *Distoloceras spinosissimum* (Hausmann). Ventral and lateral views of BMNH–X108A, showing well-developed main ribs and thus very close to *D. hirtzi* Collignon. × 0,66. Photo: W. J. Kennedy.

section would change with uncoiling), while prior to the appearance of intercalated ribs in *D. hystrix*, the ribbing is seen to arise in pairs from umbilical tubercles, whereas in *D. spinosissimum* they are simple.

Distoloceras laticostatum Imlay is known only from tightly coiled, pyritic specimens. It is more compressed, with closer, more strongly developed ribs which may bifurcate at either the umbilical shoulder, or at mid-flank. Bifurcation of ribbing has not been recorded from *D. spinosissimum*. *Distoloceras*

capulinense Imlay is very compressed, with closer, more regular ribs, some of which branch at the lateral tubercles.

Distoloceras hirtzi Collignon, from the Lower Valanginian of Madagascar, is very similar to *D. spinosissimum*, but was said to differ in having a more elliptical whorl section, prorsiradiate and not radial ribs, and in having more strongly developed midlateral tubercles. These are the features shown by Spath's topotype example, BM–C32194, and any differences are probably due to the better preservation of the Madagascan material. Consequently, *D. hirtzi* is considered a junior subjective synonym of *D. spinosissimum*.

Occurrence

Distoloceras spinosissimum is known from the Upper Valanginian of South Africa, Madagascar, and possibly England.

Distoloceras cf. *irregulare* Imlay, 1938
Figs 201–202

Compare
Distoloceras irregulare Imlay, 1938: 577, pl. 14 (figs 3, 5, 8–11).

Material

A single specimen, SAM–PCU1613, from an unknown locality.

Holotype

The original of Imlay's (1938) plate 14, figures 8–11, from the Taraises Formation of northern Mexico.

Description

In this fragment of an uncoiled example, the whorl section is subtrigonal, the flanks converging to the narrow, arched venter, the greatest width being at the dorsolateral shoulder. The dorsum, which was not in contact with the previous whorl, shows a furrowed median ridge from which initially radial, but soon becoming strongly rursiradiate, growth lines arise. Also on the dorsum, and arising from this median ridge, are very weakly developed rursiradiate ribs which strengthen towards the dorsal shoulders where they form distinct bullae. On the flanks the ribbing is rather variable, generally being prorsiradiate, although one rib is radial, and bending forwards near the venter. Between main ribs are 2–4 intercalated ribs which are prominent only across the venter. The tuberculation on the ribbing is rather variable and asymmetrical. There may be umbilical, lateral, ventrolateral and siphonal tubercles. A spine on one flank may be completely absent on the opposite side, or represented only by a weakly developed node. Siphonal tubercles are not developed on all ribs and may occasionally be eccentrically placed. The strength of the ribbing is also highly variable, fading and swelling at random. Ribs occasionally bifurcate from a lateral node.

Fig. 201. *Distoloceras* cf. *irregulare* Imlay. Front, ventral and lateral views of an uncoiled fragment, SAM–PCU1613. × 0,66.

Discussion

The solitary fragment from the Sundays River Formation is very close to *D. irregulare* Imlay, the latter differing only in having an elliptical whorl section and almost radial ribbing. It would seem that the development of siphonal spines is an ontogenetic feature as evidenced in the holotype of *D. irregulare*.

This specimen differs from *D. spinosissimum* (Hausmann) in having a subtrigonal and not polygonal whorl section, in possessing siphonal tubercles, and in the lack of regularity in the tuberculation.

Occurrence

Distoloceras irregulare Imlay is recorded from the middle part of the Upper Member of the Taraises Formation in Mexico, considered by Imlay (1938) to be of Lower Hauterivian age, and may also be present in the Sundays River Formation.

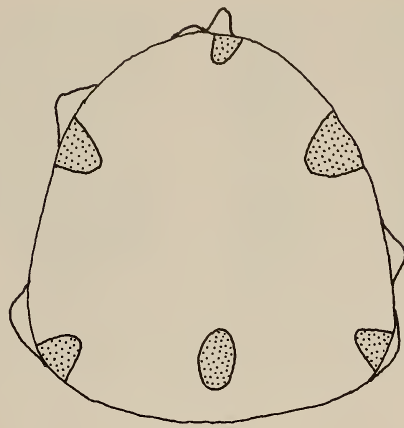

Fig. 202. *Distoloceras* cf. *irregulare* Imlay. Whorl section of SAM–PCU1613. × 0,66.

Superfamily HOPLITACEAE Douvillé, 1890

Family **Desmoceratidae** Zittel, 1895

Subfamily Eodesmoceratinae Wright, 1955

Genus *Eodesmoceras* Spath, 1924

Type species *Ammonites celestini* Pictet & Campiche, 1858; by original designation of Spath, 1924

Discussion

Two subgenera are recognized within this genus (Wright *in* Arkell *et al.* 1957), viz. *E.* (*Eodesmoceras*) and *E.* (*Miodesmoceras*). *Miodesmoceras* is a Barremian form, distinguished from *Eodesmoceras* in being more compressed and in lacking constrictions, whilst the latter is considered of Valanginian–Lower Hauterivian age. *Eodesmoceras haughtoni* Spath from the Uitenhage Group lacks constrictions, and is much more compressed than the type of *E.* (*Eodesmoceras*) *celestini* (Pictet & Campiche). Consequently, the differences between these two subgenera blurr and they appear to be of little taxonomic use.

Eodesmoceras haughtoni Spath, 1930

Fig. 203

Eodesmoceras haughtoni Spath, 1930: 141, pl. 13 (fig. 2a–e). Du Toit 1954: 384.

Material

The holotype, SAM–227, is the only specimen known.

Fig. 203. *Eodesmoceras haughtoni* Spath. Ventral, front and lateral views of the holotype, SAM–227, preserved as an internal mould. × 2.

Holotype

By monotypy, the original of the specimen figured by Spath (1930, pl. 13 (fig. 2a–e)) from '. . . Shore of pan, Zoutpan, Uitenhage', and now in the South African Museum.

Diagnosis

A compressed, immature *Eodesmoceras* in which the only ornament is very faint sigmoidal growth striae. Constrictions are lacking.

Description

The holotype is small, preserved as an internal mould, and rather involute, the outer whorl covering about two-thirds of the preceding whorl. The shell is strongly compressed with broad, flat flanks converging slightly to the narrow evenly rounded venter. At 14 mm diameter the specimen is still entirely septate. Constrictions are lacking, whilst Spath presumably observed the growth striae on the inner whorls where the shell material was preserved. The specimen has since been glued together and this feature could not be verified.

Measurements

No.	D	H	Wi	W/H	Ui
SAM–227	14	8	5	0,63	3 (21)

Discussion

Despite the fact that Spath (1930: 142) considered this species '. . . probably represents merely the inner whorls of a larger form like *Eodesmoceras celestini* (Pictet & Campiche)', he still described it as a new species.

The very small size of *E. haughtoni* makes comparison difficult. It is more compressed than the type of *E. celestini*, but this is possibly ontogenetic variation since the latter is 28 mm in diameter. According to Wright's (*in* Arkell *et al.*

1957) diagnosis of *E.* (*Eodesmoceras*), presumably based on the type species *E. celestini*, constrictions are present although they are not visible in the illustration of the lectotype. Lack of comparative material does not allow for a definite statement on the validity of Spath's species.

Occurrence

This species is known only from the Sundays River Formation.

Subclass DIBRANCHIATA Owen, 1832

Order DECAPODA Leach, 1818

Suborder BELEMNOIDEA Naef, 1912

Family **Belemnitidae** D'Orbigny, 1845

Subfamily Belemnopsinae Naef, 1922

Genus *Belemnopsis* Bayle, 1878

Type species *Belemnites sulcatus* Miller;
by subsequent designation of Douvillé, 1879

Belemnopsis africana (Tate, 1867)

Fig. 204

Belemnites africanus Tate, 1867: 151, pl. 7 (fig. 2). Kitchin, 1908: 225.
Belemnopsis africana (Tate) Spath, 1930: 155. Besairie, 1930; pl. 11 (fig. 12). Spath, 1939, pl. 24 (fig. 15). Stevens, 1965: 164.
Non Belemnopsis africana (Tate) Besairie, 1930, pl. 23 (figs 6–7, 20–21).

Material

A single unnumbered specimen in the South African Museum.

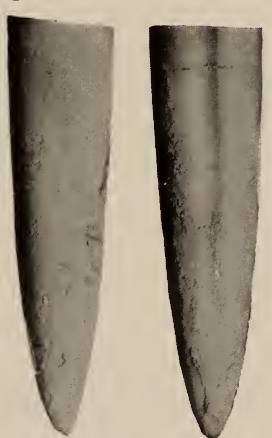

Fig. 204. *Belemnopsis africana* (Tate). Lateral and ventral views of an apical fragment in the South African Museum. × 1.

Holotype

By monotypy, the original of the specimen figured by Tate (1967, pl. 7 (fig. 2)), from the Sundays River, now in the British Museum.

Diagnosis

Guard non-hastate, expanding slowly adorally. Ventral groove deep and broad, prominent throughout growth. Cross-section depressed.

Description

The following description, based on the holotype, is taken from Stevens (1965: 164): '. . . the guard is non-hastate, its diameter gradually increasing forwards. The ventral groove, broad and deep, is very prominent throughout the growth stages of the guard. Cross-sections throughout the length of the guard are depressed (maximum transverse diameter, 19 mm: maximum sagittal diameter, 18 mm).'

Discussion

The genus *Belemnopsis* is characteristic of the Kimmeridgian–Tithonian of the Indo-Pacific, with a relict fauna surviving in South Africa and Madagascar until the late Valanginian. Spath (1930: 156) remarked that an alveolar fragment of *B. africana* could not be distinguished from *B. gerardi* Oppel (= *B. uhligi* Stevens).

The examples referred by Besairie (1936) to this species are considered by Stevens (1965) as probably distinct. They differ from Tate's species in being more elongate and slender, with an elongate sharply pointed apical region, while the ventral groove is not as deep.

The rarity of this species in the Uitenhage Group led Stevens (1965: 164) to '. . . suggest derivation from Upper Jurassic strata, since removed by erosion. However, the holotype is quite well preserved and not corroded so is probably not derived from older strata.'

Belemnopsis gladiator Willey (1973: 33, fig. 2) from the Berriasian of Antarctica is very close to Tate's species. According to Willey, *B. africana* differs in being somewhat shorter, comparatively more robust, with a deeper, flat-bottomed ventral groove with concave sides and sharp margins. The differences are, however, slight and since *B. africana* is still known only from a handful of fragmentary specimens, probably would not stand up were a population of individuals known. This is supported by the fact that Willey (1973) assigned an apical fragment of *Belemnopsis* from the Sundays River Formation, in the British Museum, BM–C6217, to *B. gladiator*. *Belemnopsis africana* may prove, therefore, to be longer ranging than is generally suspected.

Occurrence

Belemnopsis africana is known from the Lower and Upper Valanginian of Madagascar, the Upper Valanginian of South Africa, and possibly the Berriasian of Antarctica.

Order NAUTILOIDEA Agassiz, 1847

Suborder NAUTILINA Agassiz, 1847

Family **Nautilidae** de Blainville, 1825

Genus *Eutrephoceras* Hyatt, 1894

Type species *Nautilus dekayi* Morton, 1834;
by subsequent designation of Hyatt, 1894.

Eutrephoceras uitenhagense Spath, 1930

Fig. 205

Nautilus sp. Sharpe, 1856: 201. Kitchin, 1908: 225.
Eutrephoceras uitenhagense Spath, 1930: 139.
Nautilus (*Eutrephoceras*) ?*uitenhagense* Spath, Besairie, 1936: 145.

Material

The holotype is still the only specimen recorded from the Sundays River Formation.

Holotype

The specimen recorded by Sharpe (1856: 201) from the Sundays River now in the British Museum (BM–11034, Geol. Soc. Coll.).

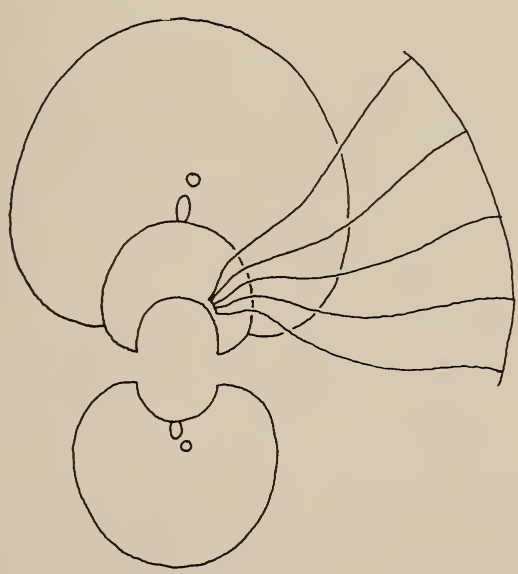

Fig. 205. *Eutrephoceras uitenhagense* Spath. Whorl section and suture (after Spath 1930). × 0,66.

Diagnosis

'Coiling occlusal, with umbilicus nearly closed. Whorl section rounded, slightly compressed at first, later flaring, with greatest thickness at inner third and no edge to high umbilical wall. Suture line with slight umbilical saddle and shallow lateral lobe, straight across venter. Annular lobe strongly developed. Test entirely smooth, thick' (Spath 1930: 139).

Measurements

No.	D	H	W	W/H	U
BM–11034	135	55	74	1,35	7 (5)

Discussion

The excentric position of the ventral siphuncle in this species was thought not to be significant by Spath (1930). He compared this species with '*Nautilus*' *boissieri* Pictet, from which *E. uitenhagense* was distinguished by its greater inflation.

Occurrence

This species is known only from the Sundays River Formation and perhaps Madagascar.

SUMMARY

The cephalopod fauna from the Sundays River Formation is revised and shown to comprise the following species:

AMMONOIDEA

Partschiceras rogersi (Kitchin)
Bochianites glaber Kitchin
Bochianites africanus (Tate)
O. (*Olcostephanus*) *atherstoni* (Sharpe) (♂ and ♀)
O. (*Olcostephanus*) *densicostatus* (Wegner) sp. juv.
O. (*Olcostephanus*) *rogersi* (Kitchin) (♂ and ♀)
O. (*Olcostephanus*) *victoris* Spath (♀)
O. (*Olcostephanus*) *fascigerus* Spath (♀)
O. (*Olcostephanus*) aff. *durangensis* (Cantu Chapa) (♂)
O. (*Olcostephanus*) *baini baini* (Sharpe) (♂ and ♀)
O. (*Olcostephanus*) *baini* var. *sphaeroidalis* (Spath) (♂ and ♀)
O. (*Olcostephanus*) *ventricosus* (Von Koenen) (?♀)
O. (*Olcostephanus*) *uitenhagensis* (Kitchin) (♀)
O. (*Olcostephanus*) *riccardii* sp. nov. (♀)

O. (*Olcostephanus*) *astieriformis* (Böse) (♀)
O. (*Olcostephanus*) *coahuilensis* Imlay (♀)
O. (*Olcostephanus*) cf. *perinflatus* (Matheron) (♀)
Neohoploceras subanceps (Tate)
Distoloceras spinosissimum (Hausmann)
Distoloceras cf. *irregulare* Imlay
Eodesmoceras haughtoni Spath

COLEOIDEA

Belemnopsis africana (Tate)
Belemnopsis gladiator Willey

NAUTILOIDEA

Eutrephoceras uitenhagense Spath

The fauna is dominated by species of *Olcostephanus*, within which sexual dimorphism is recognized for the first time from these beds. The fact that three morphologic types—microconch, macroconch, and inner whorls of the macroconch—may be distinguished within a single species (dimorphic pair), together with occasional gerontic individuals, has led to a proliferation of nominal species. This, together with complete disregard for intraspecific variation, has led to taxonomic chaos.

A literature review of sexual dimorphism in ammonites reveals that the inner whorls of many macroconchs (♀) are indistinguishable from their microconch (♂) counterparts. This, together with the occurrence of rare aberrant mutants (Cope 1967: 53), supports the contention that some sexually dimorphic ammonites display consecutive hermaphroditism or protandrism.

Many microconch species of *Olcostephanus* exhibit parabolae, as do the immature growth stages of the corresponding macroconch. Not only are parabolae virtually identical, morphologically, to the peristome but they also have an identical mode of formation. Consequently, parabolae in *Olcostephanus* are interpreted as relict peristomes. Accepting this suggestion, it is of interest to note that the whorls of many extant gastropods are ornamented with varices, representing the position of relict apertures developed during pauses in growth. They would appear, therefore, to be homologous to the parabolae occurring in *Olcostephanus*. The fact that in extant Gastropoda varices are known to be of specific importance supports the contention that they were of equal significance in *Olcostephanus*.

A significant feature associated with sexual dimorphism in *Olcostephanus* is the striking degree of convergence in the outer whorls of macroconch forms. Since *O. atherstoni* (Sharpe) was one of the earliest such macroconchs to be described, this name consistently crops up in the older literature when, in fact, the inner whorls show a different species to be involved. It is probably also this homoeomorphy which has led to the neglect of parabolae as a specific criterion.

The importance of a knowledge of the early ontogenetic stages of macroconchs for their specific determination cannot be over-emphasized, as well as being imperative for the recognition of the microconch dimorph. A slight, but apparently consistent, difference between microconch forms and the inner whorls of their macroconch appears to be a somewhat higher rib density in the latter.

The subfamily Olcostephaninae is reviewed and considered to include the following genera and subgenera: *Saynoceras* (*Saynoceras*), *S.* (*Ceratotuberculus*), *Olcostephanus* (*Olcostephanus*), *O.* (*Subastieria*), *O.* (*Parastieria*), *O.* (*Jeannoticeras*), *O.* (*Mexicanoceras*), *Jeanthieuloyites*, *Valanginites*, *Capeloites*, and *Dobrodgeiceras*. The genera *Holcostephanus*, *Astieria*, *Rogersites*, *Taraisites* and *Satoites* are considered junior synonyms of *Olcostephanus* s.s., whilst *Maderia* and *Lemurostephanus* comprise a heterogeneous assemblage of *O.* (*Olcostephanus*) and perhaps *O.* (*Subastieria*) nuclei, and are thus superfluous. In order to incorporate the new subgenera, the diagnosis of *Olcostephanus* as given by Wright (*in* Arkell *et al.* 1957) is emended. The new genus *Jeanthieuloyites* is proposed for *Rogersites quinquestriatus* Besairie.

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6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:
comma separates author's name and year
semicolon separates more than one reference by the same author
full stop separates references by different authors
figures of plates are enclosed in parentheses to distinguish them from text-figures
dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype
SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51′S 25°39′E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '. . . the Figure depicting *C. namacolus* . . .'; '. . . in *C. namacolus* (Fig. 10) . . .'

(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene

(c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as
'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

M. R. COOPER

REVISION OF THE LATE VALANGINIAN CEPHALOPODA FROM THE SUNDAYS RIVER FORMATION OF SOUTH AFRICA, WITH SPECIAL REFERENCE TO THE GENUS *OLCOSTEPHANUS*